

**SEX-SPECIFIC BEHAVIOURAL AND PHYSIOLOGICAL RESPONSES OF
BREEDING ATLANTIC PUFFINS *FRATERCULA ARCTICA* AND THEIR
CHICKS TO FLUCTUATING PREY ABUNDANCE**

by

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ABSTRACT

The Witless Bay Ecological Reserve in Newfoundland and Labrador is home to the largest breeding colony of Atlantic puffins *Fratercula arctica* in North America. Studying parental investment over several years of fluctuating prey abundance, in combination with experimental food supplementation studies, can help determine how puffins are adjusting to ecosystem changes and can reveal the potential consequences of these changes for long-term survival and reproductive success.

Puffins adopt a conservative breeding strategy such that parents need to balance their own survival and self-maintenance with parental investment, which is more challenging when food resources are low. First, how variation in resources affects chick growth and physiology was investigated. Food supplemented chicks had higher mass gain than controls, as well as higher rates of structural growth, a result previously seen only under the poorest feeding conditions. Second, audiovisual recordings and Passive Integrated Transponder tags were used to identify sex differences in parental provisioning effort, revealing that females provisioned chicks more frequently than males when food resources were low. Third, several physiological measurements were taken to determine the potential fitness consequences of parents to changing food availability. Female parents with chicks that were not food supplemented had higher beta-hydroxybutyrate levels, and indication of fasting, than both control males and adults with food supplemented chicks. These findings support the hypothesis that females invest more effort in provisioning and indicating that energetic demands of chick rearing may be greater for females than for males. Fourth, whether chick behaviour can influence

parental provisioning was investigated. Chicks produced screech calls to inform parents of their hunger levels and screech calls were reduced after food supplementation. Parents did not return to the burrow with food quicker when screech calls were produced during the previous visit, as a parent's response was limited by food availability.

The behavioural and physiological responses to variations in food availability have demonstrated the ability of parents to adjust to changing environmental conditions while balancing self-maintenance and reproductive success. Puffins in this study population have successfully endured deteriorating foraging conditions; however, long-term shortages and mismatches in prey availability during chick rearing could potentially impact future populations, as observed in declining European colonies.

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CHAPTER 1 – INTRODUCTION AND OVERVIEW

1.1 AVIAN PARENTAL INVESTMENT

The amount of investment parents provide to offspring varies within the animal kingdom. For avian species, parental duties can include securing a nesting site, incubating eggs, provisioning, protection from predators, and guidance in learning how to forage after fledging. So-called R-selected species, like most songbirds, have shorter lifespans with a high mortality rate, and have few reproductive events with multiple offspring, and low offspring survival (Krohne 2001). Conversely, K-selected species, like seabirds, have longer lifespans with a low mortality rate, many reproductive events with few offspring per event, and high offspring survival (Krohne 2001). Altricial offspring, such as those produced by most passerine species, have limited mobility and are dependent on parents for food and warmth. Precocial offspring, such as those produced by Anseriformes (e.g. ducks), can thermoregulate and find food on their own, soon after hatching. Most seabird offspring are semi-precocial, with some mobility and ability to thermoregulate, but depend on their parents for food (Clutton-Brock 1991).

Avian mating systems range from monogamy to polygamy, but 90% of avian species are monogamous (Lack 1947), if not genetically than socially (Ligon 1999). Monogamy is often associated with biparental care, in which both parents share in the responsibilities of offspring care (Ligon 1999). Although both males and females gain from a monogamous relationship, there is often conflict within the pair because each is trying to maximize its own inclusive fitness (Trivers 1972). In conditions where food is

widely and randomly distributed or limited, shared parental care is essential for the successful fledging of offspring (Clutton-Brock 1991). If one of the parents abandons the breeding attempt, the offspring will often not survive (Ligon 1999), and therefore there is a high incidence of monogamy and biparental care in seabird species (Griffith et al. 2002).

1.2 PARENT-OFFSPRING CONFLICT

Parent-offspring conflict theory suggests that parents invest in their offspring to increase the chance that their genes successfully transfer to future generations, but conflict arises when continued care of current offspring compromises their investment in future offspring (Trivers 1974, Clutton-Brock 1991). The optimum investment for parents is lower than the optimum investment that offspring demand (Trivers 1974), and conflict arises because offspring demand more resources from parents than parents are selected to provide (Trivers 1974, Parker & MacNair 1978, 1979, MacNair & Parker 1979, Clutton-Brock 1991).

1.3 SEABIRD LIFE-HISTORY

Seabirds are predominantly monogamous and have long-term pair bonds with mates. Life-history characteristics of most seabirds include delayed age of first breeding, small clutch sizes, long incubation periods, and long life spans (Schreiber & Burger

2002). Seabirds are adapted to value long-term survival over current reproductive success if breeding conditions are not ideal (Bókonyi et al. 2009).

Seabirds are important ecological indicators of changes in the marine environment and the overall health of our oceans (Cairns 1988). seabirds are useful for examining parental investment, as their primary parental duty is to provision offspring, a behaviour that can be quantified and experimentally manipulated. As many seabird chicks are semi-precocial, provisioning of offspring is one of the most important, but also time consuming and costly duties for seabird parents.

1.4 SEX DIFFERENCES

Parental investment is costly in terms of energy spent on raising offspring, which reduces time spent on self-maintenance (Trivers 1972). Costs are incurred separately to each parent, but the benefit of rearing an offspring to fledging is shared. Conflict therefore arises between partners as they try to minimize their own investment while taking advantage of benefits from their partner's effort (Trivers 1972, Jones et al. 2002).

The division of parental roles and the amount of investment from each parent is an important aspect of offspring survival. It is common in many seabird species to share certain roles of parenting, as a single parent would not be able to raise offspring on their own (Clutton-Brock 1991, Jones et al. 2002). Many seabirds are also sexually monomorphic (i.e., body size and plumage are similar between the sexes). It is predicted that due to these similar traits, there would be little specialization in their parental roles

(Ligon 1999); however, there appears to be a some variation in roles between sexes and among species.

Foraging strategies and rates of chick provisioning vary greatly between males and females across seabird species. In a study of Little Auks *Alle alle* breeding off the west coast of Norway, both males and females use a bimodal foraging strategy, in which they alternate between short and long trips between the nest and foraging sites. The duration of long trips, interpreted as self-feeding trips, was greater for females than males. These longer trips benefited female fitness, and resulted in male-biased provisioning (Welcker et al. 2009). Alternately, a study on Atlantic Puffins *Fratercula arctica* in Newfoundland found that females provisioned chicks more often, while males spent more time in mating efforts, such as mate guarding and extra-pair copulations (Creelman & Storey 1991). Male and female Wilson's storm petrels *Oceanites oceanicus* did not differ in the amount they provisioned chicks, however different foraging strategies were used by each sex. In years when food was not abundant, males made shorter duration trips with smaller meal sizes, whereas females made longer duration trips and returned with heavier meals (Gladbach et al. 2009). Although there were no sex-specific differences in investment, there was a sex-specific division in provisioning strategy. These studies demonstrate how varied the single role of provisioning can be between sexes. Among long-lived seabirds, high costs of foraging may impose an additional constraint, such that individuals may not be willing or able to extend parental investment to satisfy offspring demands.

1.5 ECOLOGICAL/FORAGING CONDITIONS

Newfoundland and Labrador is an ideal location to study seabirds, as there are many breeding colonies surrounding the province (Montevecchi & Tuck 1987). Many seabirds, such as puffins, are central place foragers and rely on abundant prey near their breeding colony to reduce lengthy foraging trips for provisioning and self-maintenance (Schreiber & Burger 2002).

A reduction in cod stocks in the Northwest Atlantic in the early 1990s closed the Newfoundland and Labrador cod fishery, which coincided with a decline in the overall biomass of the groundfish community (Pedersen et al. 2017). The cod population has not yet recovered despite the fisheries closure, and a regime shift in the marine ecosystem has resulted in low biomass and abundance of most groundfish since the cod stock collapse (Buren et al. 2014, Pedersen et al. 2017). While there has been a slow recovery of biomass and composition of other groundfish populations, including important forage fish such as capelin *Mallotus villosus* and sand lance *Ammodytes dubius*, populations have not recovered to pre-collapse levels.

The abundance of capelin, an important prey species for many seabirds (Carscadden et al. 2002), has been historically low compared to levels prior to the cod stock collapse (Buren et al. 2014, Rideout & Ings 2018). Inshore capelin spawning has also been variable and a mismatch in timing of breeding with availability of nearby food resources has complicated provisioning effort of seabird parents (Doody et al. 2008, Regular et al. 2008; 2014, Wilhelm et al. 2008, Rector et al. 2012, Storey et al. 2017). Capelin migrate offshore during winter and return to inshore waters to spawn, which traditionally

coincided with seabird chick hatching in Newfoundland and Labrador (Cairns 1987, Carscadden et al. 2002), but has not always matched hatching and chick rearing in recent years (Doody et al. 2008, Wilhelm et al. 2008, Regular et al. 2014).

Sand lance are also an important food resource for breeding seabirds in the Atlantic Ocean (Rodway & Montevecchi 1996, Baillie & Jones 2003; 2004, Burke & Montevecchi 2008, Rector et al. 2012, Regular et al. 2014, Veit & Manne 2015). As there is no commercial fishery for sand lance, there is little monitoring of their population and therefore, information about abundance is scarce. The information that is available is from offshore trawl surveys beginning in 1995 and shows no obvious trends over the years (Rideout & Ings 2018). However, abundance levels are low during the time series for the years of the current study (2010-2013). Offshore abundance does not necessarily translate to inshore abundance; however, it does represent the biomass that is potentially available, and offshore abundance of capelin has been used to predict later inshore abundance in previous studies (e.g., Storey et al. 2017).

While the chapters in this thesis mainly discuss the availability of capelin as prey, the general biomass of fish in the region, which includes both capelin and sand lance, is low and has not returned to levels that existed prior to the collapse of fish stocks that occurred in the early 1990s.

1.6 STUDY SPECIES AND STUDY AREA

This thesis focuses on Atlantic puffins *Fratercula arctica*, a long-lived seabird belonging to the family Alcidae. Atlantic puffins are the only puffin species that reside in

the North Atlantic Ocean (the two Pacific species are horned *F. corniculata* and tufted *F. cirrhata* puffins). The Atlantic puffin (hereafter puffin) has breeding colonies in the north eastern part of North America, as well as Greenland, Iceland, Norway, Ireland, Russia, Scotland and other parts of Europe (Lowther et al. 2002, Harris & Wanless 2011). Greater than 90% of the global population resides in European countries and the puffin was recently listed as Vulnerable on the International Union for Conservation of Nature (IUCN) Red List (Birdlife International 2017). In North America, the largest breeding population of puffins is in the Witless Bay Ecological Reserve in Newfoundland and Labrador. Four islands make up the reserve, including Great, Gull, Green and Pee Pee Islands. Puffins breed in burrows, which are dug into the soil on the slopes of the island. Population estimates for Gull and Great Islands in the early 1980s indicated approximately 182,000 breeding pairs and increased to approximately 347,000 breeding pairs in the early 2000s. Current population estimates for Gull and Great island is approximately 293,000 breeding pairs, and approximately 8,000-11,000 breeding pairs reside on Green and Pee Pee Islands, which are smaller islands that are difficult to land on to obtain population estimates (Robertson et al. 2004, Wilhelm et al. 2015).

This research took place on Gull Island, which is located at 47°16'N, 52°46'W and is approximately 0.8 km² in size. In addition to puffins, the island has a large population of other breeding seabirds, including Leach's storm petrels *Oceanadroma leucorhoa*, common murrelets *Uria aalge*, razorbills *Alca torda*, herring gulls *Larus argentatus*, great black-backed gulls *Larus marinus*, black-legged kittiwakes *Rissa tridactyla*, and the occasional black guillemot *Cepphus grylle* and northern fulmar *Fulmarus glacialis* breeding pairs. Black-backed gulls prey on adult puffins and herring gulls steal food

from provisioning puffin parents. Other occasional predators are American mink *Neovision vision* and bald eagles *Haliaeetus leucocephalus*.

Puffins are monogamous and typically retain the same mate for several years. They reach sexual maturity at age 4-5 years and breed each summer raising a single offspring. Eggs are laid in early May and are incubated by both parents for approximately 40 days. Chicks hatch in late June and early July and fledge from their nest after 38-44 days. Time is only spent at the colonies during the breeding season, as they spend their winters at sea (Lowther et al. 2002, Harris & Wanless 2011).

1.7 THESIS GOALS AND CHAPTER OUTLINE

Studies on Atlantic puffins have explored the effects of variable foraging conditions on parental investment (Barrett & Rikardsen 1992, Erikstad et al. 1997, Eilertsen et al. 2008), the consequences of increases and decreases to parental care (Johnsen et al. 1994, Erikstad et al. 2009), sex-specific parental duties (Creelman & Storey 1991), and the influence of chick begging on parental provisioning (Rector et al. 2014). However, my study is the first of a series of studies to combine multiple factors and explores the interactive relationship between sex-specific parental investment and chick responses with natural and experimental variations in feeding conditions.

To investigate parental investment, experimental manipulations to reduce parent effort have removed one parent, handicapped a parent, or used foster chicks to investigate how parents respond (e.g. Johnsen et al. 1994, Weimerskirch et al. 1995, Bertram et al. 1996, Erikstad et al. 1997, 2009, Takahashi et al. 1999a, Takahashi et al. 1999b, Harding

et al. 2002, Velando & Alonso-Alvarez 2003, Jacobs et al. 2013). Alternatively, food supplementation studies have been used to investigate the response of parents to a perceived increase in their partner's efforts, with previous studies showing mixed responses from partners who either reduce or maintain parental effort (Hudson 1979, Cook & Hamer 1997, Tveraa et al. 1998, Wernham & Bryant 1998, Takahashi et al. 1999a, Takahashi et al. 1999b, Gjerdrum 2004, Dahl et al. 2005).

I designed two separate food supplementation studies that were conducted over a four-year period. Study 1 (Figure 1.1) was conducted in 2010 through 2013 and the data are included in Chapters 2 and 4. Study 2 (Figures 1.2 and 1.3) was conducted in 2011 and 2012 and those data are included in Chapters 3 and 5. These experimental manipulations combined with natural prey availability were used to inform the following hypotheses:

- 1) Food supplementation improves chick growth and condition in this colony and reduces parent provisioning effort;
- 2) Female parents invest more in provisioning effort of offspring than males;
- 3) Higher provisioning effort by females results in higher physiological costs for female compared to male parents; and
- 4) Parental provisioning effort is influenced by chick begging calls

This thesis is organized in manuscript form. Chapter 2 is based on a published manuscript in Marine Ecology Progress Series and focuses on chick physiology and growth. Chapter 3 focuses on sex differences in parental investment. Chapter 4 focuses on sex differences in the physiology of breeding adults. Chapter 5 focuses on parent-chick

communication and behaviour. Chapter 6 consists of an integrated discussion of the previous chapters.

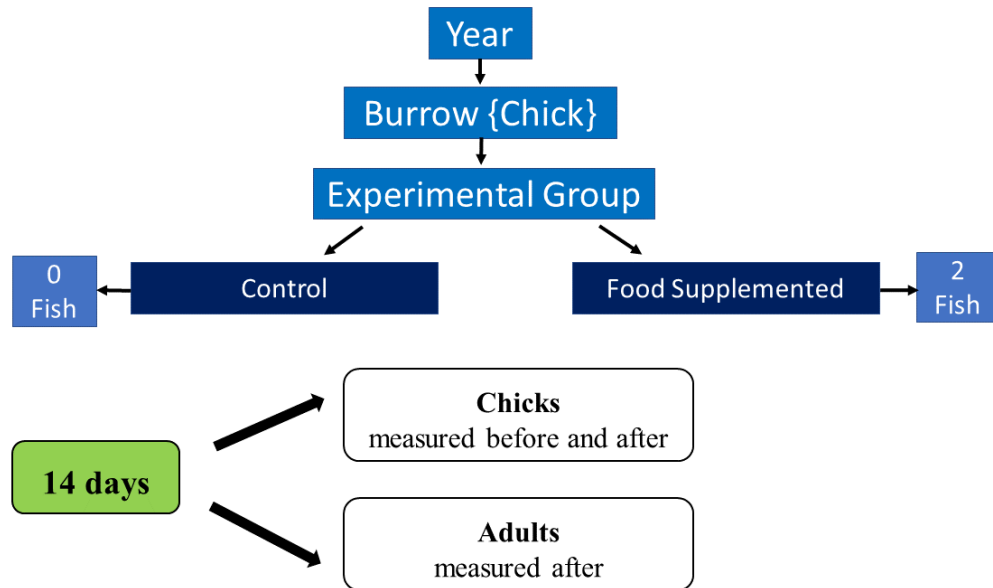


Figure 1.1. Experimental design and timeline of Study 1

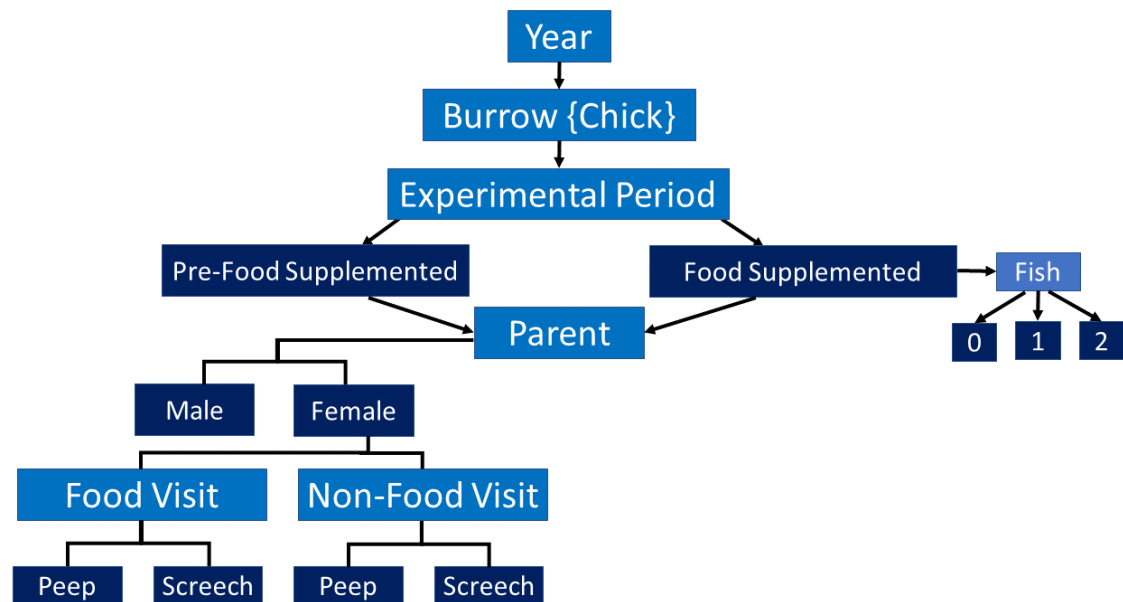


Figure 1.2 Experimental design of Study 2

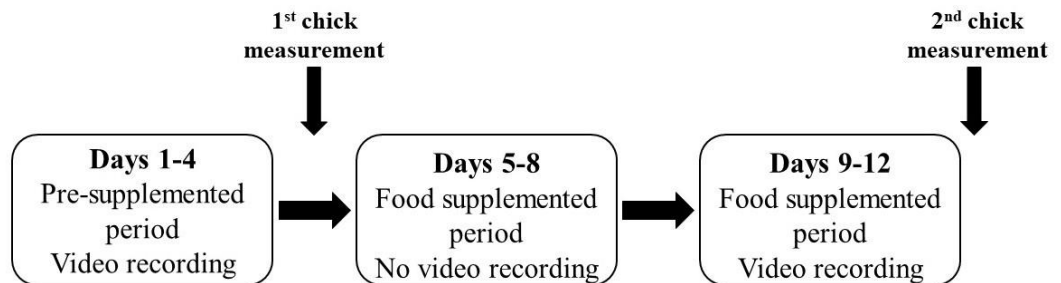


Figure 1.3 Timeline of audio and video recordings of Study 2

1.8 CO-AUTHORSHIP STATEMENT

This thesis is the result of a PhD project in the Cognitive and Behavioural Ecology Programme at Memorial University of Newfoundland. Principal financial and logistical support was provided by my supervisor Dr. Anne Storey (NSERC Discovery Grant and

Research Tools and Instruments Grants Program). Substantial logistical support for fieldwork was provided by Dr. Gregory Robertson, Dave Fifield, and Dr. Sabina Wilhelm (Environment and Climate Change Canada) and Ecotours Zodiac Adventures. Lab space and technical support was provided by Dr. Donald McKay, Dr. Gene Herzberg, Dr. Carolyn Walsh, and the Genomics and Protonomics (GAP) Lab (Dr. Elizabeth Perry, Linda Tao and Brettney Pilgrim), as well as Dr. Rod Byrne and Dave Fifield (for technical support with the Passive Integrative Technology tag system).

1.8.1 Design and identification of the research proposal

Research questions, design of methods, and the proposal of research were developed by Michelle G. Fitzsimmons, in collaboration with Dr. Anne Storey. Drs. Carolyn Walsh, Colleen Barber and Gregory Robertson provided guidance and suggestions throughout.

1.8.2 Practical aspects of the research

The coordination and collection of all field data (behavioural observations, blood samples, and measurements of birds) was conducted by Michelle G Fitzsimmons, with the assistance of numerous field assistants (see Acknowledgements). Design and construction of the Passive Integrative Technology tag system was done by Dr. Rod Byrne. Implementation and technical support of the system was done by Michelle G Fitzsimmons, with the guidance of Dr. Rod Byrne and Dave Fifield. Determination of corticosterone levels in blood via radioimmunoassay were done by Michelle G Fitzsimmons, Megan Rector and Amy-Lee Kouwenberg, with the guidance of Dr. Don

McKay. Determination of beta-hydroxybutyrate levels in blood via colorimetric assay were done by Michelle G Fitzsimmons and Morag Ryan, with the guidance of Dr. Gene Herzberg. Determination of genetic sex in birds via blood samples were done by Michelle G Fitzsimmons, with the guidance of technicians in the GAP lab.

1.8.3 Data analysis

All statistical analyses were performed by Michelle G Fitzsimmons, with the support and guidance from Dr. Anne Storey, Dr. Dave Schneider, Dr. Gregory Robertson, Dave Fifield and Paul Regular.

1.8.4 Manuscript preparation

Michelle G. Fitzsimmons wrote all text, interpreted all results, prepared all tables and figures and took all photographs presented within this thesis. Thesis chapters were greatly improved by revisions and suggestions provided by Drs. Anne Storey, Carolyn Walsh, Colleen Barber and Gregory Robertson (all chapters), Dr. Donald McKay and three anonymous reviewers (Chapter 2) and Dave Fifield (Chapter 3). Relevant co-authors are identified at the beginning of each thesis chapter.

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CHAPTER 2 - HIGH GROWTH AND LOW CORTICOSTERONE IN FOOD-SUPPLEMENTED ATLANTIC PUFFIN *FRATERCULA ARCTICA* CHICKS UNDER POOR FORAGING CONDITIONS

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2.1 ABSTRACT

Prey availability surrounding seabird breeding colonies is often unpredictable, with prey fluctuating in both abundance and distribution. This study examined the effects of natural and experimentally altered food intake on chick growth and physiological condition in Atlantic puffin *Fratercula arctica* chicks during three breeding seasons. Previous studies have shown that food-supplemented chicks generally do not gain more mass than control chicks because parents of food-supplemented chicks reduce their provisioning effort in response to the decreased food requirements of their offspring. In contrast, food-supplemented chicks in this study gained significantly more mass per day and had greater tarsus and wing growth than control chicks. Consistent with available information on capelin spawning, our results suggest that prey availability was generally so poor that parents could not reduce provisioning effort, even when extra food was provided, as chicks were being fed the minimum amount for development. Corticosterone was significantly higher in control chicks compared to food-supplemented chicks, which is consistent with some but not all previous studies. Chicks had lower mass when prey availability was poor, but this was associated with high corticosterone levels only when weather conditions were also poor. These results suggest that measuring multiple fitness indices can be useful for determining overall environmental conditions and can provide insight into how puffins are adjusting to changes within their ecosystem.

2.2 INTRODUCTION

Environmental conditions surrounding seabird breeding colonies are often unpredictable, with prey availability fluctuating in both abundance and distribution. Atlantic puffins *Fratercula arctica* raise a single offspring per year, as part of a conservative strategy to maximize their long-term survival (Bókonyi et al. 2009, Breuner 2011). Having some flexibility in their parental investment, parents adjust their effort depending on their own condition and the food requirements of their offspring in response to foraging conditions (Johnsen et al. 1994, Erikstad et al. 1997, 1998, 2009, Williams et al. 2008, Rector et al. 2012).

Atlantic puffins in Newfoundland and Labrador are generalist foragers but feed their chicks mainly capelin *Mallotus villosus*. When capelin are less available, puffins forage on sand lance *Ammodytes dubius* and larval fish. In years when prey are smaller, less abundant, or are less nutritious, parents may increase the provisioning rate or the numbers of prey collected, so that offspring still receive a comparable diet (Burger & Piatt 1990, Eilertsen et al. 2008, Kadin et al. 2015). Increasing provisioning rates to compensate for low quality food requires increased energy expenditure and can negatively affect adult survival and future reproductive success (Wernham & Bryant 1998, Davis et al. 2005, Breton & Diamond 2014, Elliott et al. 2014, Kress et al. 2016). If parents cannot increase provisioning effort, chick condition and fledging success may be lower (Barrett & Rikardsen 1992, Kress et al. 2016), and the risk of parental abandonment is greater (Johnsen et al. 1994, Erikstad et al. 2009). Capelin, which is more energy dense than larval fish (Montevecchi & Piatt 1984, Lawson et al. 1998), has

decreased by 90% in population abundance in offshore Newfoundland waters since the early 1990's (Buren et al. 2014, DFO 2015), and there has been a decline in size and age at spawning (Carscadden & Frank 2002). The abundance and timing of inshore capelin spawning has also shown considerable variation (Carscadden et al. 1997, Carscadden & Frank 2002, Regular et al. 2008, 2014, Rector et al. 2012, DFO 2015), influenced by seasonal sea ice dynamics that have impacted the overall marine ecosystem (Buren et al. 2014). Consequently, proportions of capelin in the diets of puffin chicks in Witless Bay have declined, and parents have not necessarily compensated by increasing provisioning rates (Table 2.1).

Chick growth and physiological condition can be effective indicators of food availability during the breeding season (Cairns 1988, Piatt et al. 2007, Rector et al. 2012). When food is limited, chick mass gain can be slow while structural growth is generally maintained (Robinson et al. 2002, Moe et al. 2004). Only when food availability is extremely poor, are both chick mass gain and structural growth rates lower (Øyan & Anker-Nilssen 1996, Kitaysky 1999). Secretion of corticosterone (CORT), the primary glucocorticoid in birds, can mediate trade-offs of energy allocation and resources between reproduction and survival during challenging situations (Bókony et al. 2009, Breuner 2011, Crespi et al. 2013). Traditionally thought of as a response to stress (Wingfield et al. 1998), changes in CORT levels can help maintain stability through stressful situations, performing more as an anti-stress hormone (Wingfield & Kitaysky 2002, McEwen & Wingfield 2003). Increases in CORT levels can be beneficial or costly to an individual depending on the duration and amount of CORT increase, as well as the environmental conditions and life history of the species (Romero et al. 2009, Breuner 2011). High

CORT levels have been associated with decreased food availability in adult seabirds (Kitaysky, Wingfield, et al. 1999, Kitaysky et al. 2007, Doody et al. 2008, Barrett et al. 2015). For seabird chicks, the association between CORT levels and food limitations is less straightforward. Tufted puffin *Fratercula cirrhata* chicks that were food-deprived had no elevation in CORT levels (Kitaysky et al. 2005, Williams et al. 2008), whereas other seabird chicks had higher CORT levels when food availability was low (black-legged kittiwake, *Rissa tridactyla*, Kitaysky, Piatt, et al. 1999; red-legged kittiwake, *Rissa brevirostris*, Kitaysky et al. 2001; rhinoceros auklet, *Cerorhinca monocerata*, Sears & Hatch 2008; Caspian tern, *Hydroprogne caspia*, Patterson et al. 2015). Elevated CORT levels in chicks in moderately stressful situations may increase begging (Kitaysky et al. 2001, Quillfeldt et al. 2006), resulting in increased provisioning from parents. However, if parents are unable to respond appropriately to chick begging or if chick provisioning is irregular, CORT levels may decrease or remain low to avoid the detrimental effects of chronic CORT elevations (Kitaysky et al. 2005). The variation in results may also be due to both the differing degrees of poor foraging conditions in each study, and possibly species-specific adaptations in physiological responses to food shortages.

Studies that experimentally increase parental provisioning effort can measure a chick's response to limited food conditions. Parental provisioning effort has been increased experimentally by removing one parent (Weimerskirch et al. 1995, Takahashi et al. 1999a, Takahashi et al. 1999b), prolonging the chick rearing period by substituting younger chicks (Johnsen et al. 1994, Bertram et al. 1996, Erikstad et al. 1997, 2009), handicapping one or both parents (Weimerskirch et al. 1995, Velando & Alonso-Alvarez 2003, Harding et al. 2009, Jacobs et al. 2013), or increasing brood size (Velando &

Alonso-Alvarez 2003, Bortolotti et al. 2011). However, if parents do not have the ability to increase effort because natural food resources are too limited, then an experimental design in which parental provisioning effort is potentially reduced by supplementing chick food intake is a more useful method to evaluate how limited food conditions influence chick growth and physiology.

Supplemental feeding experiments in previous studies have been used to reduce parental effort, demonstrating that in most situations, parents will alter their provisioning based on the food requirements of their offspring (Tveraa et al. 1998, Takahashi et al. 1999b). If supplemented food (in addition to that provided by parents) is above the necessary amount for chicks to maintain growth, then parents can reduce their provisioning. It has been demonstrated in several puffin studies that food-supplemented chicks do not gain more mass than control chicks (Hudson 1979, Wehle 1983, Cook & Hamer 1997, Wernham & Bryant 1998, Gjerdrum 2004, Dahl et al. 2005). Food-supplemented chicks initially gained more mass than control chicks in one study (Harding et al. 2002), but parents began reducing their provisioning to the supplemented chicks after six days into the experiment.

We conducted a preliminary study that indicated that supplemental fed chicks gained more mass than control chicks fed only by their parents (Rector 2011). The supplemental feeding regime appeared to be insufficient to detect any measurable effects on parental provisioning, because either the foraging conditions were really poor or not enough supplemental food was provided. There was no difference in CORT levels between the two groups; however, the supplemental feeding only lasted for one week, which may have not been enough time for any differences to develop. The current study

was modified to increase the length of time and the amount of food provided, and it was conducted over three breeding seasons. We predict that (1) mass gain will be greater in food-supplemented compared to control chicks, when prey availability was poor; (2) structural growth will not differ between food-supplemented and control chicks; and (3) CORT levels will be higher in chicks that were fed less (control chicks and/or during poor prey availability years) than chicks that were fed more (food-supplemented chicks and/or during good foraging years).

Table 2.1 Frequency of capelin in Atlantic puffins *Fratercula arctica* chick diet and daily provisioning rates of parents in Witless Bay, Newfoundland and Labrador, Canada

Source	Island	Year	Frequency of capelin %	Provisioning rate d ⁻¹
Creelman and Storey 1991	Gull	1985	63	4.5
Rodway and Montevecchi 1996	Great	1993	44	n/a
Baillie and Jones 2003	Gull	1997	34	n/a
Baillie and Jones 2003	Gull	1998	45	n/a
Rector et al. 2012	Great	2001	22	n/a
Rector et al. 2012	Great	2002	52	n/a
Rector et al. 2012, 2014	Gull	2009	18	2.5

* n/a = no data available

2.3 METHODS

2.3.1 Study site

This study was conducted on Gull Island, in the Witless Bay Ecological Reserve, Newfoundland and Labrador, Canada (47°15' N, 52°46' W) during May to August 2011 through 2013. The entire reserve supports an estimated 300,000 breeding pairs of Atlantic puffins, with approximately 120,000 pairs breeding on Gull Island (Robertson et al. 2004, Wilhelm et al. 2015).

2.3.2 Experiment

Approximately 50 burrows with eggs were located and marked in May or June of each year. Each burrow was checked for hatching every two days from late June through early July. Some burrows were selected after chicks had hatched, and their ages were estimated from a regression of age on wing length of chicks of known age (as in Rodway 1997). Chicks that either died or were unreachable by the researcher were excluded from the study. All chicks were of comparable age and size in each group at the start of the experiment (Table 2.2). The supplemental feeding experiment began in mid-July when chicks were approximately 15-20 days old. Chicks were weighed using a 500 g Pesola scale, and wing and tarsus lengths were measured once at the beginning of the experiment and again at the end of the experiment. The growth measurements coincide with the linear growth phase (chicks continue to grow/gain mass until approximately 7-10 days before fledging, Harris & Wanless 2011; all chicks in the experiment fledged at least 10 days

after the last growth measurement). The difference between the two measurements was divided by the number of days in the experiment to derive a measure of daily growth.

Chicks in the experiment were either fed two capelin (~30 g total provided by Fisheries and Oceans Canada [DFO]) each day (in addition to food provided by parents) or were part of an unfed control group (undisturbed or disturbed by placing a hand in the burrow). At the end of the experiment, 0.5 cc of blood was taken and dropped onto a blood spot card (Whatman, GE Healthcare Life Sciences) for the CORT analysis. CORT concentrations were determined using COAT-A-COUNT Rat CORT ¹²⁵I radioimmunoassay kits (Cat. #TKRC1, InterMedico, Markham, Ontario) with modifications for measurements using blood spot cards (see Doody et al. 2008 for procedure). Intra-assay CVs were 5.50-5.89% and inter-assay CVs were 9.5-17.2%. Values between years were adjusted relative to the standardized sample in each assay for any between-year comparisons to account for the yearly assay variation; however, analyses on the non-adjusted CORT values yielded the same overall results.

Eight samples with handling times exceeding the recommended limit of 3 min (Romero & Reed 2005) were excluded from the analysis. Results remained unchanged whether these samples were included or excluded. Blood spot CORT values were converted to serum values of ng.ml⁻¹ (using the equation described and validated in Rector et al. 2012) when reported in the tables/figures to allow for comparisons of CORT values in other studies.

Table 2.2 Age (in days, means \pm SE), sample size, and summary of ANOVA indicating no difference in chick size between experimental groups at the start of the experiment

Year	Age	N	Mass (g)		Tarsus (mm)		Wing (mm)	
			<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
2011	17.11 \pm 0.29	44	0.52	0.597	0.22	0.805	0.37	0.693
2012	15.41 \pm 0.33	44	0.92	0.408	1.56	0.222	0.34	0.715
2013	15.19 \pm 0.51	36	2.43	0.104	2.34	0.112	1.78	0.184

2.3.3 Assessment of yearly differences in capelin timing and availability

No estimates are available for inshore capelin spawning timing for the Witless Bay area, however estimates from Bellevue Beach in Trinity Bay (80km away, 47° 38' 2" N, 53° 45' 59" W) provided by DFO have been used previously to approximate capelin spawning in Witless Bay. In previous studies, assessments of when capelin were available to chick-rearing birds using inshore spawning information has been supported with seabird breeding data (Doody et al. 2008, Regular et al. 2008, 2014, Wilhelm et al. 2008, Rector et al. 2012, Storey et al. 2017). Puffins feed on capelin spawning schools and will continue to mainly forage inshore, even once capelin have dispersed (Piatt 1990, Shoji et al. 2015), which makes inshore capelin spawning activity a good estimate of available food for chick provisioning. As seen in Table 2.3, capelin had completely dispersed from inshore areas by mid-chick rearing in both 2011 and 2013, whereas capelin activity was distributed across the chick-rearing period in 2012. In addition, chick hatch dates were on average much later than peak spawning activity in 2013, producing a resource/breeding mismatch. Due to these yearly differences in capelin availability, we factored year into

our analysis to assess for different natural feeding conditions, in addition to the different experimental feeding conditions.

Table 2.3 Mean chick hatch dates and inshore capelin spawning information from Fisheries and Oceans Canada (DFO)

Year	Mean chick hatch dates	Peak capelin spawning	Spawning activity period
2011	July 1	July 5	June 26-July 20
2012	June 30	July 14	June 15-August 12
2013	July 9	July 3 & 22	June 16-July 8 & July 22-24

2.3.4 Statistical analyses

The effects of the experimental feeding group and year on mass gain, tarsus growth, wing growth, and CORT were analyzed using separate univariate GLM and Tukey post-hoc comparisons when appropriate. The effect of year on CORT in relation to mass gain was analyzed using an ANCOVA, and yearly relationships of mass gain, tarsus growth, and wing growth with CORT were tested using Pearson correlations. Tests of normality (Shapiro-Wilk test) for CORT values were significant, indicating that these values were not normally distributed; therefore, CORT values were log transformed for all analyses. There was no difference between the disturbed and undisturbed control groups for any of the daily growth measures or for CORT, therefore these two groups were combined as the control group for all analyses. Means are expressed as ± 1 SE. All comparisons are two-tailed, and differences were considered significant when $p < 0.05$. All statistical analyses were performed using SPSS, version 23.0 (IBM, Armonk, NY, USA).

2.4 RESULTS

2.4.1 Chick growth

Food-supplemented chicks gained more mass per day than control chicks, $F_{1,118} = 52.68$, $p < 0.001$. Chicks gained more mass per day in 2012, compared to 2011 and 2013, $F_{2,118} = 10.74$, $p < 0.001$. There was no significant interaction of feeding group and year, $F_{2,118} = 0.43$, $p = 0.650$ (Figure 2.1).

Food-supplemented chicks had greater tarsus growth than control chicks, $F_{1,118} = 7.41$, $p = 0.007$. Chicks had greater tarsus growth in 2012, compared to 2011 and 2013, $F_{2,118} = 11.64$, $p < 0.001$. There was no significant interaction between feeding group and year, $F_{2,118} = 0.29$, $p = 0.750$ (Figure 2.2).

Food-supplemented chicks had greater wing growth than control chicks, $F_{1,118} = 12.72$, $p = 0.001$. Chicks had greater wing growth in 2012 compared to 2011, $F_{2,118} = 3.34$, $p = 0.039$, but there was no difference in wing growth in either 2011 or 2012 compared to 2013. There was no significant interaction between feeding group and year, $F_{2,118} = 0.03$, $p = 0.967$ (Figure 2.3).

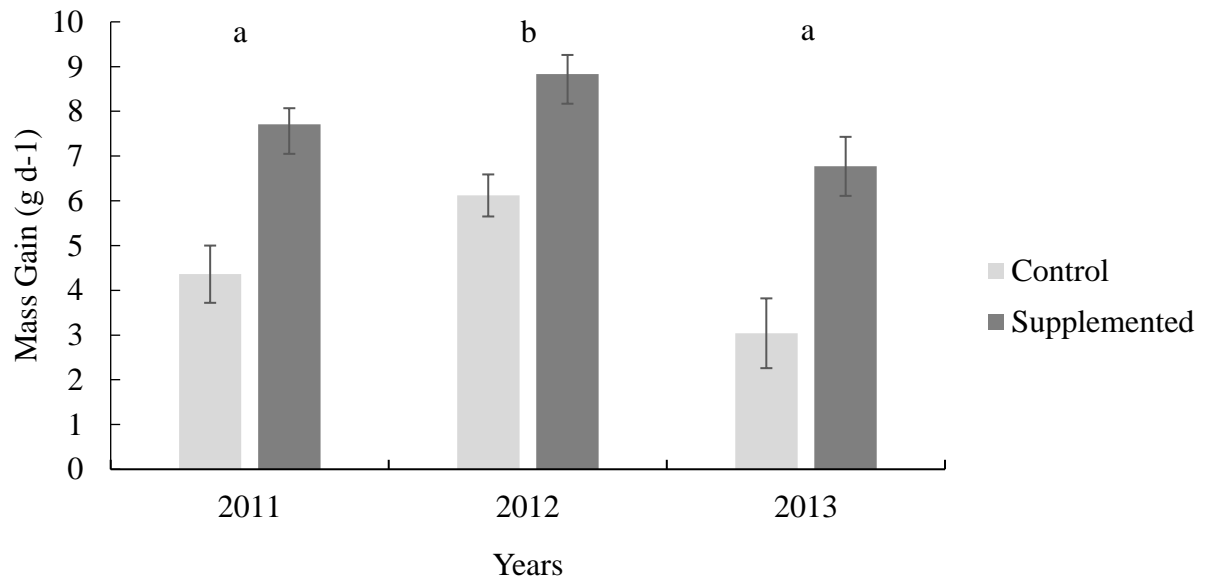


Figure 2.1 Food-supplemented Atlantic puffin *Fratercula arctica* chicks gained significantly more mass (mean \pm SE) than control chicks across all years. Different lowercase letters over pairs of bars indicate a significantly lower overall mass gain in years 2011 and 2013 than in 2012. There was no significant interaction between feeding group and year

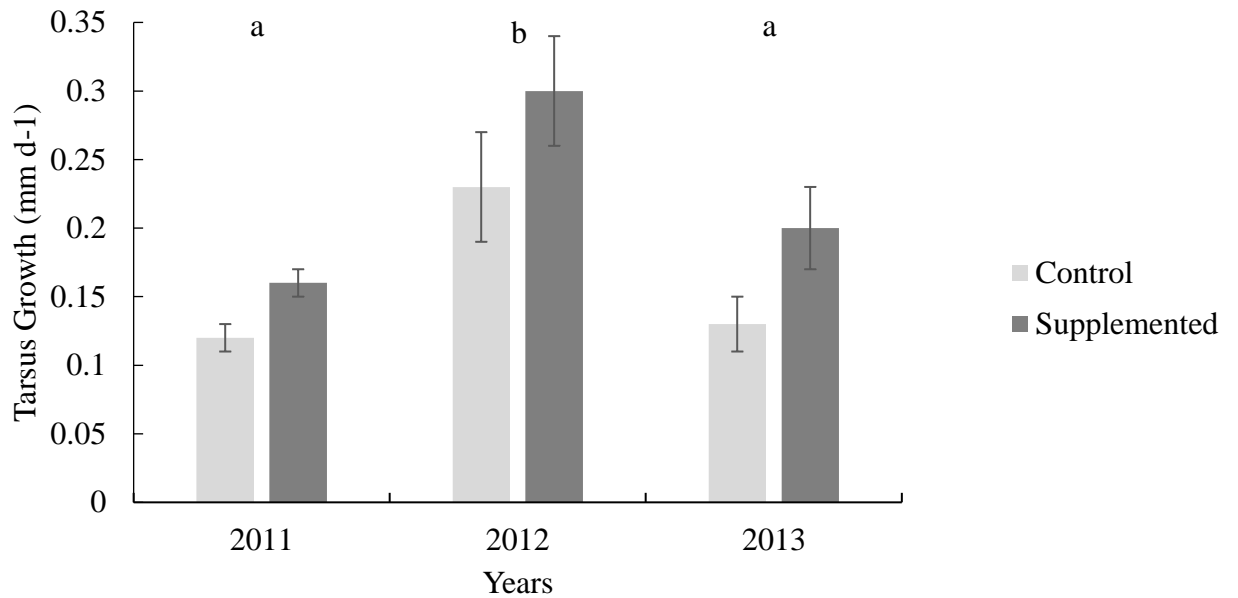


Figure 2.2 Food-supplemented Atlantic puffin *Fratercula arctica* chicks had significantly greater tarsus growth (mean \pm SE) than control chicks across all years. Different lowercase letters over pairs of bars indicate a significantly lower overall tarsus growth in years 2011 and 2013 than in 2012. There was no significant interaction between feeding group and year

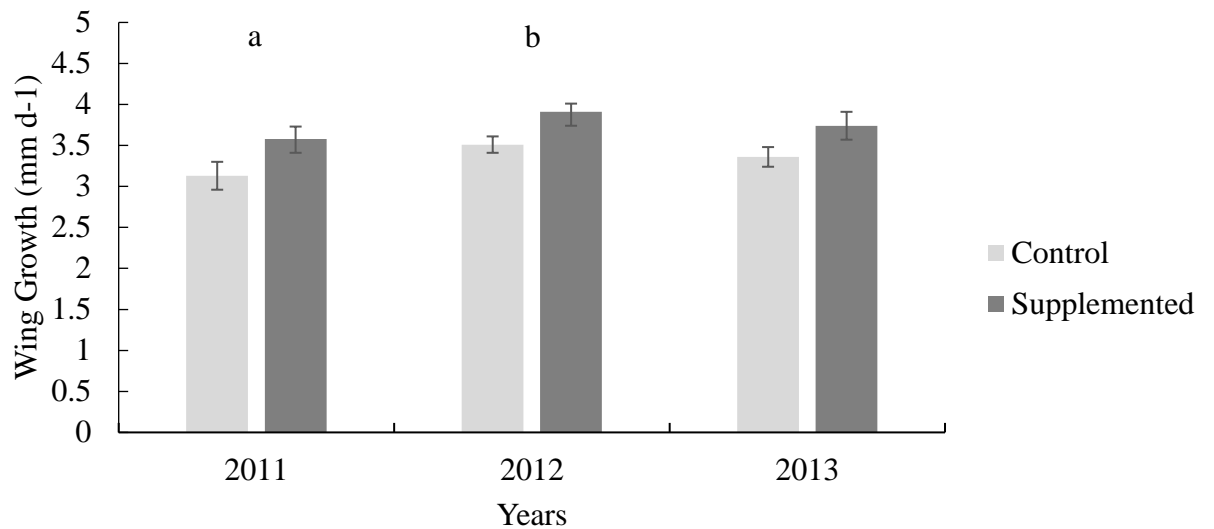


Figure 2.3 Food-supplemented Atlantic puffin *Fratercula arctica* chicks had significantly greater wing growth (mean \pm SE) than control chicks across all years. Different lowercase letters over pairs of bars indicate a significantly lower overall wing growth in the year 2011 than in 2012. There was no significant interaction between feeding group and year

2.4.2 CORT

Overall, food-supplemented chicks in all years had lower CORT levels than control chicks, $F_{1,93} = 4.48$, $p = 0.037$. There was no significant difference in CORT values among years, $F_{2,93} = 0.20$, $p = 0.811$, and no significant interaction between feeding group and year $F_{2,93} = 0.96$, $p = 0.388$ (Table 2.4).

Table 2.4 CORT levels (ng.ml⁻¹, means \pm SE) in chicks in the control and food-supplemented groups

Year	Control	N	Food-supplemented	N	All Chicks	N
2011	18.39 \pm 2.32	17	14.28 \pm 1.68	18	16.27 \pm 1.44	35
2012	15.19 \pm 1.76	16	14.46 \pm 1.12	17	14.81 \pm 1.01	33
2013	18.01 \pm 2.74	15	12.13 \pm 0.92	16	14.97 \pm 1.48	31
Overall	17.20 \pm 1.31	48	13.66 \pm 0.76	51	15.38 \pm 0.76	99

2.4.3 Chick growth in relation to CORT

There was no significant effect of year on CORT levels after controlling for daily mass gain, $F_{2,103} = 1.15$, $p = 0.322$. Within-year relationships of CORT levels and daily mass gain showed that chick CORT levels in 2011 were negatively related to daily mass gain, $r = -0.451$, $p = 0.007$ (Figure 2.4A) and tarsus growth, $r = -0.458$, $p = 0.006$ (Figure 2.4B), but there was no significant correlation with wing growth ($r = -0.225$, $p = 0.193$). There was also no significant relationship between CORT levels and growth in 2012 (mass, $r = -0.131$, $p = 0.428$; tarsus, $r = -0.138$, $p = 0.402$; wing, $r = -0.079$, $p = 0.632$) or 2013 (mass, $r = -0.177$, $p = 0.326$; tarsus, $r = 0.066$, $p = 0.715$; wing, $r = -0.062$, $p = 0.734$).

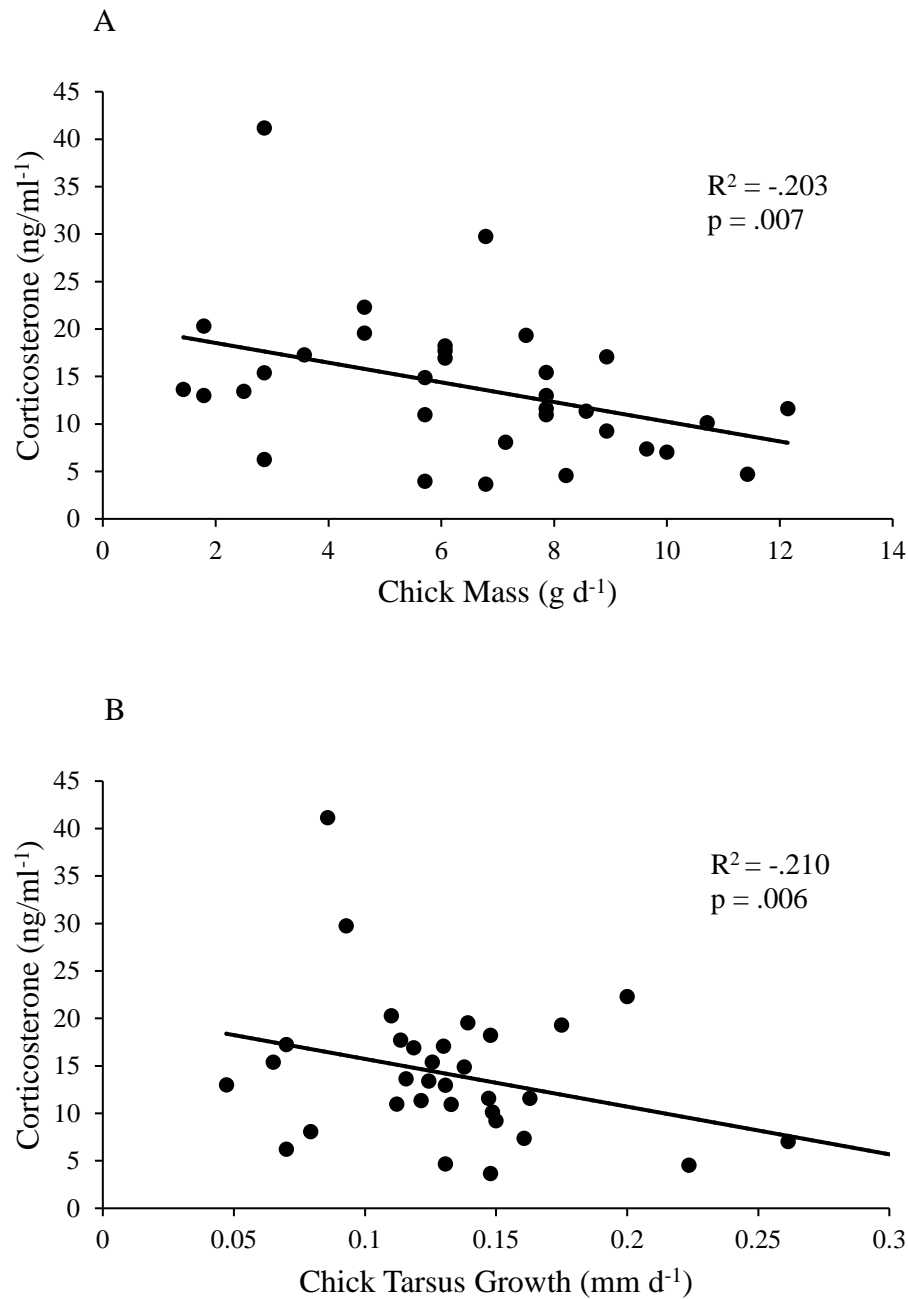


Figure 2.4 Significant negative relationship in Atlantic puffin *Fratercula arctica* chicks in 2011 between CORT levels and (A) mass gain and (B) tarsus growth

2.5 DISCUSSION

Puffin chicks in this study that were provided with supplemental food had higher mass, tarsus, and wing growth and lower CORT levels than control chicks. In addition, year differences in growth correspond with the information on capelin spawning, which suggest that prey availability was poor in 2011, good in 2012, and temporally mismatched with chick rearing in 2013. Although estimates of offshore spring capelin abundances were double in 2013 than they were in 2011 and 2012 (DFO 2015), they were still only 10% of what they were in the early 1990's. The abundance of capelin offshore does not necessarily translate into abundance of inshore capelin, with timing of inshore spawning relative to the chick rearing period being a more important factor when estimating available prey for provisioning chicks (Regular et al. 2014) as the availability of key forage species is vital for successful reproduction (Hipfner 2008, Watanuki et al. 2009).

Greater mass gain in food-supplemented chicks in this study differs from other similar experiments in that puffin parents in those studies apparently reduced their provisioning effort in response to the supplemental feeding. Parents of food-supplemented chicks in this study, however, did not reduce their provisioning, or at least not to an extent that it eliminated the significantly higher mass gain in food-supplemented chicks. As prey availability for this colony has declined in recent years, parents may still need to work hard to feed their chicks, even when meals are supplemented. Parents may have reduced their foraging effort to some degree in the better prey year (2012), as the percent increase in daily mass gain was somewhat smaller (44%) between food-supplemented and control chicks than in 2011 (77%) and 2013 (122%). However, control

chicks in 2012 still received less food from their parents (inferred from their mass gain) than control Atlantic puffin *Fratercula arctica* chicks in other supplemental feeding studies. For example, control chicks in the Cook & Hamer (1997) study gained mass at 9.43 g/day compared to 6.12g/day for control chicks in the best year (2012) of this study. Similarly, control chicks gained between 5.7 and 13.3 g d⁻¹ throughout a 25 year monitoring study in Hornøya, Norway (Barrett 2015), in which only three of the worst years in that study had chicks with marginally less mass gain than the chicks in the best year of this study.

These differences in experimental studies are a consequence of variations in food supply, which is reflected in the overall declining fledging weights of puffin chicks for this colony. Researchers were no longer in the field during fledging time, however, overall fledging success can be estimated from information collected by the Canadian Wildlife Service that measure recent puffin fledglings found on the mainland of Witless Bay (~10km from the colony; see Wilhelm et al. 2013 for methods). Only 13 chicks were captured in 2011 (mean weight of 210 g \pm 6 SE, n = 3), compared to 414 chicks in 2012 (248 g \pm 1 SE) (Wilhelm et al. 2013). In 2013, only 62 chicks were captured (236 g \pm 4 SE), with overall post-fledge mass of chicks in 2011 and 2013 lower compared to 2012 (S. I. Wilhelm unpublished data). Despite similar search efforts, very few stranded puffins were found in 2011 and 2013 compared to 2012, which may be an indication of fewer puffins having successfully fledged. Although conditions in 2012 were good, overall prey conditions for this colony have substantially declined in recent years and these declining growth rates may affect future post-fledging survival and recruitment into the population (Kress et al. 2016).

Tarsus growth was lower in both 2011 and 2013 compared to 2012, and wing growth was lower in 2011 compared to 2012. Both tarsus and wing growth were also lower in control compared to food-supplemented chicks, indicating that food scarcity was severe enough in the natural prey conditions that overall chick growth was reduced. Researchers have discussed and critiqued the use of various ratios or residuals of body mass on structural size to calculate an index of body condition (Jakob et al. 1996, Schulte-Hostedde et al. 2005, Green 2014) to determine the mass associated with energy reserves, after correcting for structural size. In this study, when food was severely limited and environmental conditions were harsh (e.g. 2011 in this study), both mass and structural size were low. The smaller size in both mass and structural components of chicks in 2011 resulted in a better body condition ratio for these chicks compared to those in 2012, despite the fact they were clearly in worse condition (2011, 2.80 g/mm vs. 2012, 2.76 g/mm; calculated as mass/tarsus). Thus, a different index of condition, such as CORT levels, may be a more valuable assessment of condition when environmental conditions are very poor.

In addition to the poor prey availability in 2011, weather conditions were also unfavorable, with many burrows leaking from excessive rainfall (150 mm of rain in July, Environment and Climate Change Canada). Cooler temperatures potentially made it difficult for the chicks to maintain regular body temperatures, as parents do not continuously brood chicks. When subjected to persistent cool and wet temperatures, body temperatures of chicks can drop from 38.5 to 31.1 °C (Vongraven et al. 1987) and metabolism rates can increase (Wilson et al. 2004). Several thousand chicks died midseason in 2011 (personal observation), and a necropsy performed on a sample of

chicks indicated starvation and hypothermia as the cause of death (L. Rogers, Veterinary pathologist, Animal Health Division, Department of Natural Resources, St. John's, NL, Canada). Low mass gain and tarsus growth were related to higher CORT in this year, although not in the other poor prey availability and mismatch year of 2013, suggesting that the association between low growth and high CORT levels in this species may occur only when environmental conditions are extremely poor.

Our finding that CORT levels were lower in food-supplemented than control chicks differs from other studies. The puffin chicks in this colony experienced greater than normal intermittent provisioning (see Table 2.1). Providing food supplementation to chicks at midday when parental provisioning rates are low likely reduced chick begging and energy expenditure, resulting in lower CORT levels in food-supplemented chicks compared with control chicks. Although elevated CORT was only associated with low mass gain in 2011, chicks in both 2011 and 2013 had low mass gain. CORT level elevations can be both beneficial and costly to chicks (Kitaysky et al. 2003) and the non-linear relationship between food intake and CORT levels even within the same species suggest that multiple factors contribute to changes in CORT levels. High CORT levels in 2011 may have facilitated begging frequency and the lower mass gain may not have been due to just the low food intake, but also to the greater energy expenditure to regulate body temperatures in the cool and wet conditions. Conversely, chicks in 2013 may have suppressed CORT elevations because the parents were not responding by increasing provisioning, as the mismatch with capelin spawning limited adult foraging efforts.

In the context of previous studies, this study demonstrates that puffins have considerable flexibility in acquiring and providing food to their chicks, however they are

ultimately constrained by resources. As long as food is above some threshold level that allows chicks to maintain growth for successful fledging, adults may adjust their foraging efforts to minimize their own workload to maintain their own condition. Chick growth can be independent of food density when prey abundance is moderate to good, with parents adjusting time budgets to feed chicks adequately, as seen in several alcid seabirds (Burger & Piatt 1990, Baillie & Jones 2004, Harding et al. 2007, Burke & Montevecchi 2008, Eilertsen et al. 2008, Wilhelm et al. 2008, Regular et al. 2014). However, when prey availability falls below critical densities, parental effort is maximized, and chick growth is then controlled by food density. Puffin chick growth can be a useful indicator of low to moderate prey conditions but provides little insight into prey density fluctuations that occur above a certain threshold of abundance. This transition from functional to uncorrelated relationships above threshold prey densities has become recognized as a fundamental characteristic of seabird-prey relationships (Piatt et al. 2007, Cury et al. 2011).

Measuring multiple fitness indices (growth, CORT, fledging success) over several years of prey fluctuations can be useful in determining how puffins are adjusting to changes within their ecosystem. Atlantic puffins in this study population have successfully endured the deteriorating foraging conditions thus far; however, long-term shortages or mismatches in prey availability with chick rearing could potentially impact future populations, as observed in other seabird breeding colonies (Barrett et al. 2006, Cury et al. 2011, Breton & Diamond 2014, Kress et al. 2016).

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CHAPTER 3 - PARENTAL INVESTMENT IN ATLANTIC PUFFINS: CHANGING PRIORITIES WITH VARYING RESOURCES

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3.1 ABSTRACT

Sex differences in parental investment have not been extensively studied in seabirds. To better understand sex differences in parental investment of Atlantic puffins *Fratercula arctica*, an experimental food supplementation study was conducted in two breeding seasons that differed in natural prey availability. Observations included 2464 hours of infra-red video recordings from 14 burrows, each filmed daily over a 12-day period. Male and female partners were identified using color bands and Passive Integrated Transponder (PIT) tags. Parents provisioned their chicks during 55.9% of all visits, while other parental duties during no-food visits included brooding, loafing and nest maintenance. Female parents provisioned chicks more often than males and there were more chick provisioning visits and no-food visits (including more frequent brooding) in the good foraging year compared to the poor foraging year. During the good foraging year, female and male provisioning rates were similar during both the pre-supplementation and food supplementation periods, with both parents reducing their provisioning visits during the food supplementation period. However, in the poor foraging year, females provisioned their chicks more often than males during the pre-supplementation period and then reduced their provisioning visits during the food supplementation period. Males, in contrast, provisioned their chicks at the same lower rate during both periods. When food resources are poor, males prioritize self-maintenance over parental investment, whereas females will invest more in chicks, potentially at the expense of their own condition. Low provisioning and brooding by parents in 2011

resulted in low chick growth and reduced productivity. The findings underline the behavioural flexibility of parents to changing food conditions.

3.2 INTRODUCTION

Biparental care in seabirds is necessary for successfully raising offspring, as reproductive costs are higher under unpredictable environmental conditions with limited resources (Clutton-Brock 1991, Ligon 1999). Parents need to balance their own survival and self-maintenance while taking care of offspring needs, which can be more challenging when food resources are low. The amount of care that parents contribute to offspring is often not as much as offspring are demanding, therefore conflict can arise not only between parent and offspring (Trivers 1974), but between partners (Jones et al. 2002).

Behavioural, physiological and environmental constraints can influence males and females differently and can alter sex-specific contributions (Trivers 1972). Although biparental care is necessary for chick-rearing seabirds, each parent's role in raising offspring can be different. During chick-rearing, the most essential and energetically costly role for parents is chick provisioning (Erikstad et al. 1997, Weimerskirch et al. 1997). However, chick provisioning needs to be balanced with self-maintenance, and a dual foraging strategy is employed by many seabird parents with longer foraging trips taken for self-feeding and shorter foraging trips for chick provisioning (Weimerskirch et al. 1997, Thaxter et al. 2009, Welcker et al. 2009, Tyson et al. 2017). Differences in foraging strategies between sexes are typically attributed to size dimorphism, foraging

efficiency and intraspecific competition. Males are typically the larger sex in sexually dimorphic seabirds and due to their greater size, they have greater foraging efficiency and can out-compete females at more productive foraging grounds (Weimerskirch et al. 1997). For example, there was no apparent sexual segregation of foraging grounds for Cory's shearwaters *Calonectris borealis* when prey availability was good. However, females fed on lower trophic prey and travelled further from the colony when food conditions near the colony were poor. As a result, female body condition and mass declined (Paiva et al. 2017). Variations in foraging strategies and abilities still emerge in the absence of large size or mass differences between sexes (Fraser et al. 2002, Lewis et al. 2002, Paredes et al. 2006, Peck & Congdon 2006). Female wedge-tailed shearwaters *Puffinus pacificus* provisioned chicks less frequently than males, but also had longer foraging trips away from the colony with more shallow dives. This difference in foraging behaviour suggests that males were out-competing females at more productive foraging grounds closer to the colony (Peck & Congdon 2006).

Investment in reproduction that occurs both prior to (e.g. egg production) and following (e.g. chick care after fledging) chick rearing can also influence behaviour during chick rearing. In one colony, male common murre *Uria aalge* made longer foraging trips and more dives per trip than females, suggesting that they prioritized self-feeding over chick feeding and exploited areas farther away from the colony for food sources. Females provisioned chicks more often than males, as males likely prioritized self-feeding in anticipation of the paternal-only care after fledging (Thaxter et al. 2009). Little auk *Alle alle* males also have post-fledging care of their chicks. However, little auk females made longer self-feeding foraging trips than males, and males provisioned chicks

more frequently than females (Welcker et al. 2009). It was suggested that the energetic expenditure of egg production for little auk females may carry over into chick rearing and thus females may prioritize self-feeding over chick provisioning, even though males have post-fledging care of their chicks. Although post-fledging paternal care was similar in both murres and little auks, provisioning effort differed between sexes. However, other studies of common murres (Storey et al. 2017) and little auks (Kidawa et al. 2015) showed no sex differences in provisioning effort, suggesting that multiple factors can influence provisioning investment.

Environmental conditions can also impact how parents invest in offspring and can modify their contributions. Crested auklets *Aethia cristatella* have distinct parental roles, with males spending more time attending the nest to protect chicks from predators, whereas females spent more time chick provisioning. Females made more frequent trips, while males brought larger prey items; thus, overall food provided was similar between males and females. However, when foraging conditions were poor, both the number of prey items and the provisioning rates of males and females were similar, but nest attendance was reduced (Fraser et al. 2002). While measuring specific parental behaviours is important, knowing the context and how parental activities interact with other factors (e.g. food availability) is essential. Measuring multiple indices, such as the quality or timing of behaviours may reveal more information about the function and context of the sex differences in parental behaviour. For example, female semipalmated sandpipers *Calidris pusilla* spent more time incubating eggs than males, allowing males more time to forage. However, males incubated during warmer temperatures when foraging efficiency was greater. This was a beneficial trade-off for partners, as females

spent more energy incubating eggs but then foraged during better conditions (Bulla et al. 2014).

Atlantic puffins *Fratercula arctica* are monogamous seabirds that depend on biparental care of their chicks (Lowther et al. 2002, Harris & Wanless 2011). Although these parents have a common goal in fledging their chicks, there may still be conflict within the relationship as each is trying to maximize its own fitness (Trivers 1974). Puffins share the duties of parental care, including incubation, nest maintenance, mate guarding and chick provisioning, although sex-specific contributions in each duty differ between and within pairs (Creelman & Storey 1991). Puffin parents can adapt to changing conditions, and still successfully fledge chicks, although this may come at a cost to their own body condition (Johnsen et al. 1994, Erikstad et al. 1997, 1998). Successful chick fledging is a combination of how well self-maintenance can be balanced with chick care (Erikstad et al. 1997). An experimental study that switched small and large chicks to increase parental effort in Atlantic puffins showed that growth was similar in experimental chicks to control chicks, as parents adapted. However, only a few parents of experimental chicks extended provisioning past the normal fledging period of their original chick, and those parents that did so were in poorer condition compared to controls (Johnsen et al. 1994).

Creelman & Storey (1991) showed that female puffins spent more time away from the colony than males during chick-rearing, but provisioned chicks more frequently. Males spent more time on mate guarding and nest maintenance than females. To expand on these findings, the current study was conducted over two years of variable foraging conditions, allowing me to measure the effects of prey availability on parental investment.

I also introduced an experimental food supplementation component to manipulate parental effort. Parental effort can either be experimentally increased (Johnsen et al. 1994, Weimerskirch et al. 1995, Bertram et al. 1996, Erikstad et al. 1997, 2009, Takahashi et al. 1999a, Takahashi et al. 1999b, Velando & Alonso-Alvarez 2003, Harding et al. 2009, Jacobs et al. 2013) or decreased (Hudson 1979, Wehle 1983, Cook & Hamer 1997, Tveraa et al. 1998, Wernham & Bryant 1998, Takahashi et al. 1999a, Takahashi et al. 1999b, Gjerdrum 2004, Dahl et al. 2005). When foraging conditions are poor, experimentally decreasing parental effort is a more useful method to evaluate parental responses, as increasing effort beyond the threshold for self-maintenance may lead to abandonment of the chick.

Supplemental feeding experiments have demonstrated that parents will often decrease their provisioning effort when chicks are being fed by researchers in addition to the provisioning by their parents (Hudson 1979, Wehle 1983, Cook & Hamer 1997, Wernham & Bryant 1998, Gjerdrum 2004, Dahl et al. 2005). Supplemental feeding of chicks may influence the behaviour of both parents, but the extra food may influence their provisioning behaviour differently if one parent typically provisions more. Provisioning in Manx shearwaters *Puffinus puffinus* is typically male-dominated, with males providing 40-50% more food to chicks than females. When chicks were food supplemented, both male and female parents reduced provisioning effort proportionally to their pre-supplemental feeding effort (Hamer et al. 2006). The current study will further examine sex differences in parental provisioning during a supplemental feeding experiment, in another seabird species with documented sex differences in chick provisioning.

Using Passive Integrated Transponder (PIT) tags for identification and infra-red cameras for observations in this study improved our ability to detect provisioning rates and parental behaviour inside the burrow. I predict that (1) provisioning rates will be higher in a good prey availability year (2012) compared to a poor prey availability year (2011); (2) parents will reduce provisioning rates to chicks during the food supplemented period compared to the pre-supplemented period; and (3) females will provision chicks more frequently than males and therefore will make fewer no-food visits than males.

3.3 METHODS

3.3.1 Study Site

The study was conducted on Gull Island in the Witless Bay Ecological Reserve, Newfoundland and Labrador, Canada (47°15' N, 52°46' W) during May to August 2011 and 2012. The entire reserve supports an estimated 300,000 breeding pairs of Atlantic puffins *Fratercula arctica*, with more than 120,000 pairs breeding on Gull Island (Robertson et al. 2004, Wilhelm et al. 2015).

3.3.2 Experiment

Atlantic puffin burrows were marked with metal markers in May and June of each year if there was an accessible egg in the nest. These burrows were checked again daily in early July for hatching. Burrows with chicks that were at least 10 days old (in the linear growth phase, Rodway 1997) were selected for the study (2011: N = 11, mean age = 15.2 days; 2012: N = 13, mean age = 14.3 days). The start of video-taping in new burrows

ranged from July 9 to August 1 in 2011 and July 5 to July 26 in 2012. If hatch date was unknown (2011: N = 6; 2012: N = 6), growth measurements were used to assess approximate age of the chicks separately for each year, using a technique developed at this colony by regressing age on wing length of chicks of known age (see Chapter 5; Rodway 1997).

At least one adult in each of the study burrows was captured prior to the start of the experiment and had a Passive Integrated Transponder (PIT) tag attached to a color band secured to one leg and a United States Fish and Wildlife Service (USFWS) metal band secured to the opposite leg. Individuals were weighed, tarsus and wing measurements were taken, and 0.5 cc of blood was sampled from the brachial vein and dropped onto a blood spot card (Whatman, GE Healthcare Life Sciences). Blood spot cards were dried for at least 24 hours and were stored in plastic bags until the end of the field season, and then placed in a -20-degree Celsius freezer for storage.

Burrow scope cameras (Peep-a-Roo monochrome 1.0 diameter video probe, Sandpiper Technologies, Manteca, CA) retrofitted with omnidirectional microphones (RadioShack 33-3013) and connected to a DVR recording system (Archos AV400 Series DVR) were used to record parent–offspring interactions within active puffin burrows. Cameras were deployed in burrows for 24-hour recordings, with ~2 hours of no recordings around 0900 and 2100 hours during video uploading and battery changes. Each burrow was monitored for 8 days over a 12-day period, with the first 4 days recorded as pre-supplemented observations. Chicks were food supplemented during the last 8 days with the last 4 days being recorded. Chicks in control burrows were recorded but not food supplemented. Observation periods began at approximately 1300 hours

Newfoundland daylight time (NDT) on the first day and ended at approximately 1300 hours NDT on the 5th day resulting in 4 full days of recording per observation period. The cameras were moved to a different burrow for the 4 days in between the two observation periods to increase the sample size. Cameras were pressed into the earth wall of the burrow and the presence of the camera did not appear to influence adult behavior (e.g., the parents still entered the burrows quickly the first time they visited after the camera was installed). Chicks remained undisturbed until the end of the fifth day of videotaping when each chick was temporarily removed from the burrow at approximately 1300 hours NDT, to take tarsus, wing chord, and mass measurements. Day 5 of the experiment was also the first day of supplemental feeding. At the end of the experimental period (Day 13), the chicks were again measured (mass, tarsus and wing) and 0.5 cc of blood was sampled from the brachial vein and dropped onto a blood spot card (Whatman, GE Healthcare Life Sciences) to be used for genetic sexing.

Chicks in this study were food supplemented with 1 or 2 capelin *Mallotus villosus* each day (~20-40 g of supplemental food) or no capelin (for control burrows). In 2011, both one and two capelin were used to compare results from previous studies (using one capelin, as in Rector et al. 2014). In 2012, to ensure that the experimental treatment was having the desired effect of supplementing the diet of chicks, two capelin were added to all experimental burrows and recordings were also made in control burrows (no supplemental capelin provided). Refer to Table 3.1 for numbers of recorded burrows in final analysis.

3.3.3 Yearly Differences in Capelin Availability

Timing of inshore capelin spawning is important for chick-rearing seabirds that depend on capelin and other forage fish for provisioning their chicks (Burke & Montevecchi 2008, Hedd et al. 2010). Capelin information for the Witless Bay area is not available, however estimates from Bellevue Beach in Trinity Bay (80km away, 47° 38' 2" N, 53° 45' 59" W) provided by Fisheries and Oceans Canada (DFO) have been used previously to approximate capelin spawning in Witless Bay, and have been used in previous studies assessing the availability of capelin to chick-rearing birds (Doody et al. 2008, Regular et al. 2008, 2014, Wilhelm et al. 2008, Rector et al. 2012, Fitzsimmons et al. 2017, Storey et al. 2017). Capelin had completely dispersed from inshore areas by mid-chick rearing in 2011, whereas capelin activity was distributed across the chick-rearing period in 2012 (see Chapter 2; Fitzsimmons et al. 2017). Due to these yearly differences in capelin availability, year was factored into the analysis to account for differences in natural feeding conditions, in addition to the different experimental feeding conditions.

3.3.4 Sex Determination

Blood taken during capture was used to genetically determine adult sex. DNA was extracted from blood spot cards using a DNeasy Blood and Tissue Kit (Qiagen), and sex of both the adults and chicks were determined using a CHD (chromodomain helicase DNA)-based molecular method involving a polymerase chain reactions (PCR). The PCR method used highly conserved primers 2550F and 2718R. Females were characterized by two fragments (CHD1W and CHD1Z) and males were characterized by one fragment

(CHD1Z) following agarose electrophoresis. The protocol was based on the methods in Dawson et al. 2001.

3.3.5 PIT Tag Antennas and Readers

PIT tags (UHF RFID glass tags, 12 x 2 mm, 0.1 g, CoreRFID Ltd, UK) were attached with epoxy and monofilament to yellow or blue alpha-numeric color bands, before they were deployed on puffins. Low frequency circular antennas were placed around the outside of the burrows and were secured with metal pegs. Antennas were attached to PIT tag readers (manufactured in-house by R. Byrne and D. Fifield). PIT tag antennas were checked daily to ensure they were secured to the outside of the burrow and test PIT tags were used to confirm that the PIT tag readers were working properly. Most technical issues were resolved during that time and if they could not be resolved, detailed notes were taken about the problems. PIT tag data were uploaded from each burrow approximately every 24 hours.

3.3.6 Video Analysis

In 2011, 11 burrows were recorded, however video for one burrow was not analyzed due to complications with recording throughout the experiment. In 2012, 13 burrows were recorded. A chick from one burrow went missing, two chicks appeared frequently in another burrow (the entrances to each of their burrows were connected, as discovered later in recording), and two burrow recordings had no sound, so these four burrows were not analyzed. Four days of videos for each experimental period (pre-supplemented and food supplemented/control) comprising a total of ~1760 hours in 2011

(N = 10) and ~1584 hours of video in 2012 (N = 9) were viewed in Final Cut Pro X (v10.1 Apple Inc) and were coded for a series of behaviours during parent-chick interactions. Parental behaviour was coded for: the duration of the visit, visit type (food or no-food provided), parental activity, and the species and number of fish. In addition, I recorded whether bands were seen on the legs of the adult (USFWS metal band on one leg with a yellow or blue color band on the opposite leg, or no bands) for identifying the male and female parents.

3.3.7 Estimating Parents of Unknown Identity

At least one parent from each burrow was color banded with a PIT tag attached. The sex of the individual was determined genetically in the lab after the study. If the second parent was not captured, it was assumed that it was of the opposite sex to the one captured. Parents were identified during visits to the burrow as either banded or unbanded parent by a) observing the parent on the video and determining whether a USFWS metal band and color band were attached to the legs or b) if the bands were not visible on the video, matching the PIT tag information of the time when the tag was detected with the time when the parent was seen on the video either entering or exiting the burrow. In some instances, the PIT tags were not detected by the readers and the adult's legs were not seen during a burrow visit; therefore, the identity of the parent during this visit was not known. A non-PIT tag detection does not guarantee that the bird entering the burrow was unbanded. Tag orientation is important for detecting PIT tags, and therefore some PIT tags may be undetected. Therefore, the conditional probability of a bird being banded or

not in these instances, and therefore determining whether the bird was the male or female parent, was calculated using Bayes Theorem.

Based on prior knowledge related to visits in which the parent's identity was known (the legs of the parent were observed and/or the PIT tag was detected), the probability that the parent was an unbanded adult given that no PIT tag was detected ($\Pr(UB|NPIT)$) was determined using the following formula:

$$\Pr(UB|NPIT) = \frac{\Pr(NPIT|UB) * \Pr(UB)}{\Pr(NPIT)}$$

where $\Pr(NPIT|UB)$ is the prior probability of visits by unbanded birds with no PIT tags, $\Pr(UB)$ is the prior probability of visits by unbanded birds, and $\Pr(NPIT)$ is the prior probability of visits by birds with no PIT tag. The probability was calculated separately for each burrow to account for variation in camera set-up, PIT tag function, and puffin pair behaviour. There were an equal number of banded birds that were male or female.

Probabilities ranged from 0.00 (being the least likely to be unbanded) and 1.00 (being the most likely to be unbanded). If the probability for any given burrow was < 0.50 , the unidentified parent was coded as having a band, and if the probability was > 0.50 , the unidentified parent was coded as having no bands. Probabilities ranged from > 0.60 to < 0.38 , with a 0.79 average probability for banded individuals and 0.16 average probability for unbanded individuals. Two burrows had probabilities of 0.46 and 0.57, therefore the unidentified parent had almost an equal chance of being banded or unbanded. The same results were obtained with and without these two burrows, since only a few visits were unknown; therefore, these burrows were kept in the final analyses. Three other burrows had $> 50\%$ of visits that were unknown and therefore the probability

calculations could misrepresent the parent identity. These three burrows were excluded from the analyses (remaining videos, 2011: N = 8, 2012: N = 6; Table 3.1).

Table 3.1 Sample size of burrows recorded and total remaining in the analysis with reasons for removal from the study.

	# Burrows	
	2011	2012
Burrows initially recorded in	11	13
Removed due to:		
technical difficulties with recording	1	0
chick went missing during recording	0	1
two chicks appeared in the same burrow	0	1
sound did not work	0	2
> 50% visits with unknown sex of parent	2	1
control burrow	0	2
Total burrows in final analysis	8	6

3.3.8 Food and No-food Visits

Any time a parent attended the nest it was considered a visit. If the parent left the nest and could not be heard or detected by a PIT tag at the entrance of the burrow for more than 15 min, the next observation at the nest was considered a separate visit. Visits were identified as food or no-food visits based on whether the parent brought fish to their chick. Presence of food was only unknown in 6.3% of visits, as most of the videos were clear enough to determine whether the parents had a fish in their bill when they entered the burrow, and/or the chick was seen eating the fish. If the visit was unknown, the

conditional probability of a visit being a food or no-food visit was calculated using Bayes Theorem.

In Rector et al. (2014), it was shown that puffin chicks will emit begging calls during parental visits. One type of call, a screech call, is more likely emitted during a no-food visit (probability of 0.74) than during a food visit, whereas peep calls are more likely emitted during food visits. Based on the known visits where no-food was brought by a parent and the chick emitted a screech call, the probability of an unknown visit being a no-food visit with a screech call ($\Pr(NF|S)$) was determined using the following formula:

$$\Pr(NF|S) = \frac{\Pr(S|NF) * \Pr(NF)}{\Pr(S)}$$

where $\Pr(S|NF)$ is the prior probability of visits with screech calls during no-food visits, $\Pr(NF)$ is the prior probability of no-food visits, and $\Pr(S)$ is the prior probability of visits with screech calls. All calculations were done within burrows and only for those burrows with unknown visits.

Of the burrows that had a few unknown visits (a total of 52 unknown visits spread across 11 of the 16 burrows), the probability of a chick emitting a screech during a no-food visit ranged from 0.64 to 1.00 (except for a probability of 0.50 for one burrow with one unknown visit), with an average probability of 0.79 across all the burrows. Based on this analysis, since all screech visits had a higher probability that they were no-food visits rather than food visits, and all peep visits had a higher probability that they were food visits rather than no-food visits, all unknown visits were categorized as no-food visits when there was a screech call and food visits when there was a peep call. Overall results would remain unchanged if unknown visits were excluded.

3.3.9 Prey Items

Prey items delivered by parents to chicks were identified as capelin *Mallotus villosus* or sand lance *Ammodytes americanus* and classified as “high nutritional prey” or were identified as larvae fish and were classified as “low nutritional prey” (Lawson et al. 1998). Provisioning by parents consisted of just a single high nutritional prey item in most instances (92% of food visits). However, when multiple fish were brought in during the same visit, the number of fish was recorded and the visit was classified as “multiple” fish. Of the 30 (out of 369 visits, 8%) visits with multiple fish, only six visits consisted of 3 fish and two visits consisted of 5 fish. All other multiple fish visits consisted of 2 fish.

3.3.10 Parent Activity During No-food Visits

Parent behaviour during no-food visits was coded and classified into three categories: nest maintenance (digging at the burrow or bringing in nest material), brooding (preening/brooding the chick) and loafing (frequently entering/exiting the burrow or could be heard/detected at the entrance of the burrow). More than one behaviour could be identified during a single visit, therefore the percentage of visits with specific activities was greater than 100% (Table 3.2). Behaviours were easy to observe and classify, however the amount of time spent on each activity was difficult to determine as the parents were not always seen on the video or the video quality was poor. Therefore, only whether the behaviour was observed or not was recorded.

Table 3.2 Frequency of occurrence (%) of parent activities of males and females during no-food visits in 2011 and 2012 during the pre-supplemented and food supplemented experimental periods. More than one parental activity can occur in a single visit.

Year	Experimental Period	Parent Sex	Brooding	Loafing	Maintenance	Total No-food Visits	
2011	Pre-supplemented	Male	13 (40.6%)	21 (65.6%)	1 (3.1%)	32	
		Female	15 (42.9%)	21 (60.0%)	6 (17.1%)	35	
		Total	28 (41.8%)	42 (62.7%)	7 (10.5%)	67	
	Food Supplemented	Male	12 (37.5%)	23 (71.9%)	1 (3.1%)	32	
		Female	4 (21.1%)	16 (84.2%)	1 (5.3%)	19	
		Total	16 (31.4%)	39 (76.5%)	2 (3.9%)	51	
	2011 Total		44 (37.3%)	81 (68.6%)	9 (7.6%)	118	
	2012	Pre-supplemented	Male	31 (64.6%)	21 (43.8%)	2 (4.2%)	48
			Female	36 (57.1%)	32 (50.8%)	16 (25.4%)	63
Total			67 (60.4%)	53 (47.8%)	18 (16.2%)	111	
Food Supplemented		Male	10 (41.7%)	16 (66.7%)	3 (12.5%)	24	
		Female	14 (38.9%)	26 (72.2%)	7 (19.4%)	36	
		Total	24 (40.0%)	42 (70.0%)	10 (16.7%)	60	
2012 Total		91 (53.2%)	95 (55.6%)	28 (16.4%)	171		

3.3.11 Statistical Analyses

The effects of year, experimental period, and parent sex on provisioning rate (visits/day) were determined using a generalized linear mixed model (GLMM) with maximum likelihood and a negative binomial error distribution, using the glmmTMB package (Brooks et al. 2017) in R (R Core Team 2017). Poisson models were briefly explored as the response variable was count data, however clear overdispersion was shown due to the large variability in the response variable, and therefore a negative binomial model was more appropriate. The control burrows in 2012 were dropped from the three-way analysis that included the feeding experiment as a parameter (2 burrows, as one had already been dropped from the analysis for having too many unknowns), with a total of fourteen burrows (2011, $N = 8$ and 2012, $N = 6$) in the analysis. The one and two capelin food supplemented groups were analyzed together as there was no difference between the groups in provisioning rates, Welch's t-test, $t_{128.92} = 0.49$, $p = 0.622$. Daily provisioning rates were calculated for each parent during the pre-supplemented and food supplemented period. The range of provisioning visits per parent for each day was 0 to 6. The global model contained a three-way interaction between year, experimental period and parent sex. Julian date was included as a covariate to determine if the decrease in provisioning rates was a consequence of chick developmental stage. The amount of time spent attending the nest was included as a covariate to determine if there was a negative relationship with provisioning rate. Individual birds and burrows were included as random effects to account for within individual variation, as multiple visits were recorded by the same birds in the same burrow. The final model contained a three-way interaction, which was a significantly better model compared to the model with the same factors but

with only two-way interactions. The three-way interaction between year, experimental period, and parent sex was a significantly better model than the previous model, $\chi^2_1 = 6.15$, $p = 0.013$. All pairwise comparisons were computed from the contrasts between factors using the lsmeans package (Lenth 2016) and p value adjustments were made for pairwise Tukey comparisons. Model fit was assessed by including fixed effects, covariates, random effects and interaction terms, and using a likelihood-ratio test to remove incremental terms and compare AIC and deviance values for each model. Parent activity was analyzed using a binomial GLMM, with presence of each parent activity (loafing, brooding and maintenance) as the response variable, and year, experimental period and parent sex as the predictors. Two-sample tests for equality of proportions were used for prey item analyses. Means are expressed as \pm SE. All analyses were conducted in R version 3.4.2 (R Core Team 2017).

3.4 RESULTS

Eight pairs of adults in 2011 and six pairs of adults in 2012 were included in the final analysis. Provisioning visits by females and males during 2012, the good foraging year, were similar during both the pre-supplemented period and the food-supplemented period, with both parents reducing their provisioning visits during the food supplemented period. However, in 2011, the poor foraging year, females provisioned their chicks more than males during the pre-supplemented period and then reduced their provisioning visits during the food-supplemented period. Males, in contrast, provisioned their chicks at the same lower rate during both periods (Figure 3.1). There was a weak effect for the

interaction between sex and experimental period showed that females provisioned chicks more than males during the later (equivalent to food supplemented) period, $z = 1.88$, $p = 0.061$. The total variation accounted by the random effects of burrow and individual bird were small (<0.01). There was collinearity between Julian date and provisioning rate, $t_{278} = -3.60$, $p < 0.001$, $r = -0.21$, however this accounted for less than 5% of the variation explained in the model (Figure 3.2). Similarly, there was collinearity between Julian date and time spent attending the nest, $t_{278} = -2.87$, $p = 0.004$, $r = -0.17$, however this accounted for less than 3% of the variation explained in the model (Figure 3.3). The effect of Julian date or time spent attending the nest on provisioning rates was not significant in the model. Within the two control burrows, there was no difference in the provisioning rates between males and females ($z = 0.44$, $p = 0.659$), or between periods similar to the experimental supplementation periods ($z = 0.04$, $p = 0.971$).

There were 287 prey loads of high nutritional value (capelin/sand lance), 26 prey loads of low nutritional value (larvae fish), and 38 prey loads that could not be classified. There was no difference in the proportion of low nutritional prey loads delivered to chicks between years ($\chi^2_1 = 2.05$, $p = 0.153$) or experimental periods ($\chi^2_1 = 1.39$, $p = 0.239$); however, there was a difference between parents ($\chi^2_1 = 6.51$, $p = 0.011$) with males making more visits with low nutritional value prey loads to chicks (12.1%; 17 of 140) compared to females (4.3%; 9 of 211). Of visits with multiple prey items, there was no difference in the proportion of visits between experimental periods ($\chi^2_1 = 0.90$, $p = 0.342$) or male and female parents ($\chi^2_1 = 0.01$, $p = 1.000$); however, there was a difference between years ($\chi^2_1 = 4.40$, $p = 0.036$) with 10.1% (19 of 189) of visits having multiple

prey items during 2012, the good foraging year, compared to 3.7% (6 of 162) of visits with multiple prey items in 2011, the poor foraging year.

Over the two years, there were 351 visits with food (54.8% of total visits) and 289 no-food visits (45.2% of total visits). Food visits were shorter (18.37 ± 84.29 min) than no-food visits (61.12 ± 122.70 min), Welch's t-test, $t_{494.10} = -5.08$, $p < 0.001$. Females ($N = 153$) and males ($N = 136$) did not differ in the proportion of no-food visits, $\chi^2_1 = 0.89$, $p = 0.347$ and there was no difference in the proportion of no-food visits between 2011 ($N = 118$) and 2012 ($N = 171$), $\chi^2_1 = 1.62$, $p = 0.204$. During no-food visits, brooding occurred in 46.7%, loafing in 59.9%, and maintenance 12.8% of visits.

Brooding occurred in more no-food visits in 2012 compared to 2011, $z = 2.81$, $p = 0.029$, and in more no-food visits during the pre-supplemented period compared to the food supplemented period, $z = 2.96$, $p = 0.003$, Table 3.2. There was no difference in the occurrence of brooding during no-food visits between males and females, $z = 0.73$, $p = 0.467$. Loafing occurred in more no-food visits in 2011 compared to 2012, $z = 2.05$, $p = 0.040$, and in more no-food visits during the food supplemented period compared to the pre-supplemented period, $z = 3.11$, $p = 0.002$. There was no difference in the occurrence of loafing during no-food visits between males and females, $z = 0.25$, $p = 0.802$. There was no difference in the occurrence of maintenance during no-food visits in 2012 compared to 2011, $z = 1.285$, $p = 0.199$, or in the pre-supplemented period compared to the food supplemented period, $z = 0.57$, $p = 0.567$. However, maintenance occurred in more no-food visits for females compared to males, $z = 2.10$, $p = 0.036$ (Table 3.2).

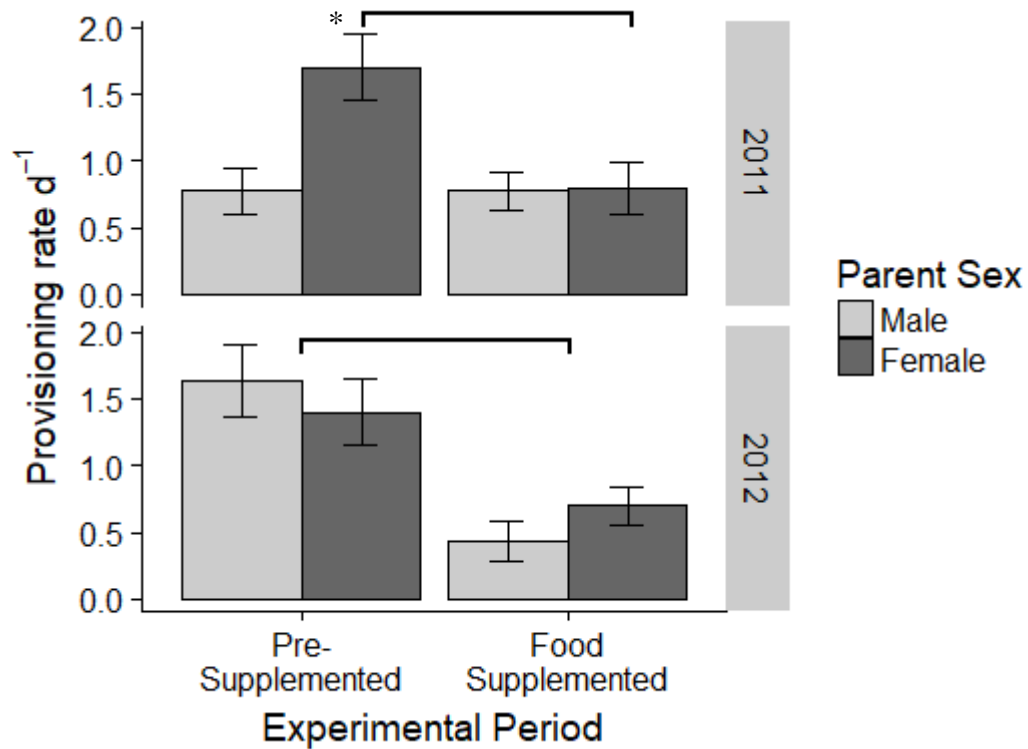


Figure 3.1 Mean \pm SE of daily provisioning rates of Atlantic puffin parents across experimental periods and year. Both male and female parents reduced provisioning from the pre-supplemented to the food supplemented period in 2012. In 2011, females provisioned chicks more than males during the pre-supplemented period, and only females reduced provisioning from the pre-supplemented to the food supplemented period, whereas males fed chicks at the same low provisioning rate during both periods.

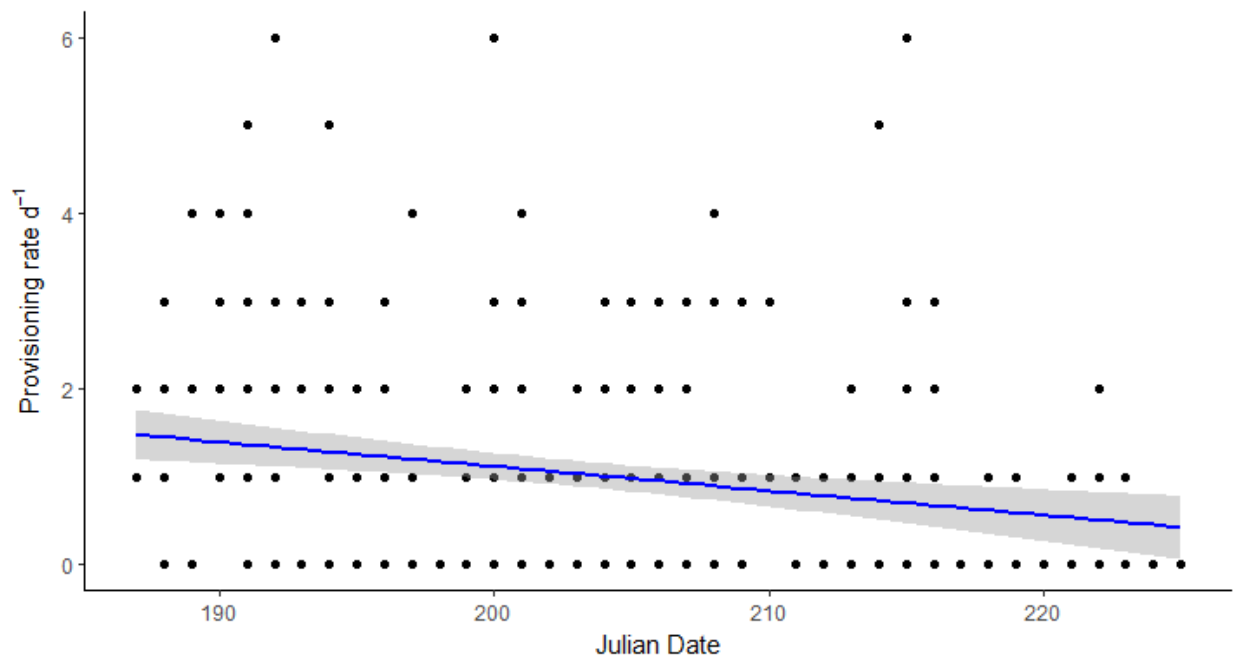


Figure 3.2 A negative relationship shows that provisioning rate (d^{-1}) decreased as Julian date increased.

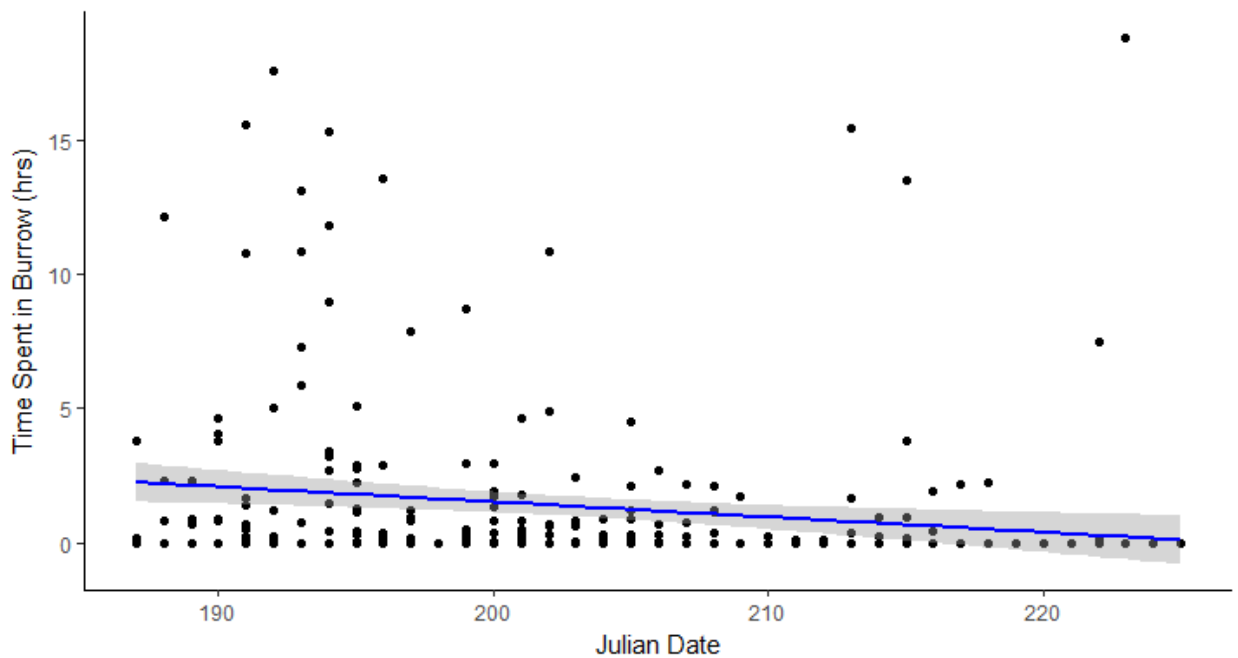


Figure 3.3 A negative relationship shows that the amount of time parents spent in the burrow decreased as Julian date increased.

3.5 DISCUSSION

Our predictions that parents provisioned their chicks more frequently in the good foraging year of 2012 compared to the poor foraging year of 2011, and that females provisioned their chicks more frequently overall than males were supported. Also, as predicted, parents reduced provisioning effort to chicks after they were food supplemented. However, the reduction in provisioning was greater in the good foraging year compared to the poor year. Females provisioned their chicks more during the pre-supplemented period in both years, and then reduced their provisioning when food was supplemented. In contrast, males provisioned their chicks at a comparable low frequency

during both pre-supplemented and food supplemented periods when the foraging conditions were poor but maintained a comparable provisioning rate to females during both periods when foraging conditions were good.

The timing of spawning and availability of prey was noticeably different during the two years of this study. Capelin had completely dispersed from inshore areas by mid-chick rearing in 2011, whereas capelin activity was distributed across the chick-rearing period in 2012. However, there was little variation in the quality of the fish provided to chicks (mostly capelin and sand lance), as well as little variation in the number of fish provided during each provisioning visit (mainly one). These results suggest that capelin and sand lance were still the main prey provided to chicks throughout the duration of the experiment, which ranged from the first week of July to the third week in August. Breeding seabirds rely on high quality prey to feed their chicks, as poor quality fish can lead to reduced reproductive success (Cohen et al. 2014). Capelin disperse farther offshore after they have spawned, and during this time parents would need to forage farther away from the colony. Another puffin study with adults carrying GPS loggers at the same colony as this study was conducted in 2016 during the first three weeks of chick rearing. Both before and after capelin had spawned, puffins bringing in capelin and sand lance were travelling up to 74 km away from the colony and were away from the colony for up to 60 hours (Isabeau Pratte, Acadia University, personal communication). This demonstrates that puffins may need to forage farther from the colony and for long periods of time, suggesting that even though 2012 was a better foraging year than 2011, inshore prey still seems less available than historically for this area (Carscadden et al. 2001, 2002). Travelling farther from the colony to obtain higher quality prey in poor foraging

years has been reported in other seabirds (Fraser et al. 2002, Burke & Montevecchi 2009, Cohen et al. 2014, Paiva et al. 2017). A higher proportion of multiple prey items in 2012 suggests that prey were more abundant and easier to catch in this year compared to 2011.

Provisioning rates declined as the season progressed, which could be due to either preferred prey being less available later in the season or prey moving farther offshore. However, experimental food supplementation period was always after the pre-supplementation period, and adults likely reduced their provisioning effort in response to the additional food that chicks were receiving, which is consistent with other supplemental feeding studies. Julian date only accounted for a small proportion of the variation in provisioning rate but was also negatively related to the amount of time spent in the burrow. Declining nest attendance can occur as the chick gets older (Maccarone et al. 2012, Rishworth et al. 2014) and parents invest more time away from the colony when foraging is more difficult (Fraser et al. 2004, Cohen et al. 2014).

Providing chicks with supplemental food can decrease the provisioning effort of parents. Previous puffin studies have shown that food supplemented chicks typically do not gain more mass than control chicks because parents adjust their provisioning rates to align with the compensated food. However, in a concurrent food supplementation study for this colony in the same years, food supplemented chicks did gain more mass than control chicks (Chapter 2; Fitzsimmons et al. 2017). Parents in this study reduced their provisioning visits during food supplementation, except for males during the poor foraging year. Since males were already provisioning at a low rate, there was not much opportunity for a further reduction. Females in both years, and both parents during the good foraging year, reduced their provisioning during the supplemental feeding period.

Although parents reduced their provisioning rate, the addition of food supplementation during this period provided chicks with more fish than previously provided by parents alone. In addition, there was no difference in provisioning rates of control parents during this period, suggesting that the decreased provisioning in the supplemental period for the experimental burrows was not age-related. Since provisioning rates are low in this colony in general, compared to historical conditions (Carscadden et al. 2002, Davoren & Montevecchi 2003, Rector et al. 2012), feeding chicks an extra one or two supplemented capelin per day was sufficient to increase chick mass and improve condition (Chapter 2; Fitzsimmons et al. 2017). Supplemental food can benefit chick growth and condition, and thus increase the value of the offspring. Parents therefore may invest more in chicks by increasing or maintaining provisioning levels, rather than decreasing provisioning during food supplementation. However, this would only be possible if sufficient resources are available.

Females provisioned chicks more often than males and this sex difference could be attributed to several factors. It is possible that males provided larger prey items to chicks to counter the higher provisioning rates of females, similar to what was found with crested auklets (Fraser et al. 2002). Measurements of larger prey items were not taken, however, the perceived size of prey observed on the videos did not differ. As the number of large prey (mostly one) provided to chicks was the same for males and females, any size differences in prey were likely not sufficient to impact the nutritional diet of the chicks, and in fact males provided a higher proportion of low nutritional prey to chicks than females. The Energetic Constraint Hypothesis suggests that males and females may contribute to parental investment differently during the chick-rearing stage due to

energetic costs during other breeding stages (Welcker et al. 2009, Elliott et al. 2010, Paiva et al. 2017), such as egg-laying (Monaghan et al. 1998) or unequal incubation (Riechert & Becker 2017). Increased burrow defense and mate guarding for males prior to chick-rearing (Creelman & Storey 1991) may increase the energetic constraints for males during chick-rearing, generating similar costs as those of egg production for females. However, the costs for males do not likely exceed the costs produced by females enough to outweigh the unequal provisioning behaviour. Females may provision chicks more during a poor foraging year due to the earlier investment by males of procuring and defending the nest. If poor foraging conditions inhibit replenishing reserves, males may focus more on self-maintenance.

Parents of food-supplemented chicks may perceive an increase in their partner's provisioning if provided with information that their chicks are in good condition (i.e., a low rate of screech begging calls, Rector et al. 2014). This perception may result in one or both partners reducing their provisioning to allow for its greater investment in self-maintenance. However, if both partners reduce their provisioning to a great extent, the decrease in food being provided will be costly to chick condition. Some other alcids, such as cliff-nesting murres, need to continuously brood their chicks or guard the nest during the chick-rearing stage, therefore taking turns to leave the nest to forage and provision (Wilhelm et al. 2008, Takahashi et al. 2017). In contrast, puffins nest in burrows, and can leave the nest unattended with little risk of predation and no need for constant brooding (Lowther et al. 2002). Parents can therefore forage for themselves and their chick with less constraint from their partner.

Coordination between partners in parental duties is essential for maximizing reproductive success. Information about a partner's investment in provisioning can help ensure the chick is being provided the food needed for development. Information can be acquired directly by observing a partner's provisioning effort (as in murrelets, Moody et al. 2005) or indirectly, through chick development and chick begging cues (as in puffins, Rector et al. 2014). Attending the nest during visits where no food is brought back to the chick may be a way for parents to observe chick condition.

Previous studies do not report the prevalence of no-food visits, likely because observing prey in the bill of a puffin while trying to enter the burrow is difficult and it was presumed by most researchers that any visit to the burrow was a provisioning visit. In Creelman and Storey (1991), 19% of visits contained unidentified prey because the birds entered the burrow too quickly. However, it is possible that there was no prey in some of those visits, and parents were just making a no-food visit. Parents do not need to defend the nest from predators or brood chicks past the first week after hatching (Lowther et al. 2002, Harris & Wanless 2011), so the purpose of spending time in the burrow may be to allow parents to monitor their partner's efforts. Loafing was the most frequent activity for both males and females, which includes frequently going in and out of the burrow and on to the slopes. This behaviour allows adults to gain information about their chicks and the behaviour of close neighbours. Brooding activity was higher for parents during the pre-supplementation compared to the food supplementation period, and in 2012 compared to 2011. Chicks were brooded on fewer visits in 2011, even though chicks would have benefited from brooding during this year, as there was persistent rain and low temperatures. As a result of the poor weather, thousands of chicks in this colony died of

hypothermia and starvation from the combined low levels of provisioning and brooding (see Chapter 2; Fitzsimmons et al. 2017).

The only significant sex difference in parental activities during no-food visits was that females performed nest maintenance in a higher proportion of no-food visits than males. In contrast, male puffins performed more nest maintenance in a previous study of puffins from this colony (Creelman and Storey 1991). However, the observations from Creelman and Storey (1991) were of maintenance outside the burrow and during the pre-laying and incubation stages, whereas the present studies observation were from inside the burrow and during chick-rearing, suggesting that nest maintenance to the burrow throughout the breeding season may be equal between partners. As for indirect observation of their partners' provisioning effort, chick-begging vocalizations are likely more useful than visual cues of chick development as the burrow is dark. Previous studies have suggested that chicks relay information about their nutritional needs through begging (Harris 1983, Rector et al. 2014, Ogawa et al. 2015). However, sex differences in parental response to these begging calls have not yet been explored in puffins (see Chapter 5).

Although the sample sizes were low in this study, limiting the statistical power of the analysis, the results were clear. Males and females have different priorities when food resources are poor. Males prioritize self-maintenance over parental investment, whereas females will continue to invest in chicks when conditions are poor, potentially at the expense of their own condition. A meta-analysis of mortality bias in 194 avian species showed that mating competition and parental care influenced only male mortality, not female. However, overall mortality was higher for females than males in that study (Liker

& Székely 2005). If investment in parental care puts males at greater risk, self-maintenance would be prioritized over provisioning effort when food resources are poor. Females may be able to carry the cost of increased provisioning, however, this may carry over past the breeding season and into winter survival (Wernham & Bryant 1998, Fayet et al. 2017). Knowing the physiological costs of increased provisioning for females (as demonstrated in Chapter 4) will provide better information about the risks associated with breeding during poor foraging conditions and the impacts to long-term survival of adults.

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CHAPTER 4 - THE COSTS AND BENEFITS OF RAISING YOUNG: A BATTLE OF THE SEXES OR INDIVIDUAL QUALITY?

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4.1 ABSTRACT

Balancing the costs of parental care requires trade-offs between self-maintenance and chick provisioning, as foraging is a costly activity for chick-rearing parents. This study measured the variation in several physiological indicators of Atlantic puffin *Fratercula arctica* parents during four breeding seasons of variable prey availability. Chicks were food-supplemented (or were unfed controls) and blood samples were taken from parents to measure beta-hydroxybutyrate (BUTY, a ketone body that elevates when there is lipid utilization and mass loss), haematocrit (a reflection of blood oxygen capacity), and corticosterone (CORT, a stress hormone). Female parents weighed less than males among parents of control chicks, but there was no sex difference in mass for parents of food-supplemented chicks. Female parents of control chicks had higher BUTY levels than female parents of food-supplemented chicks, and the only significant predictor of high chick mass gain across all years was low BUTY levels in female parents. Parents had higher haematocrit levels during the poor prey availability years, which may be related to longer and deeper dive requirements for prey. Overall parent mass was negatively correlated with CORT levels, but there were no sex differences in CORT levels. The differences in physiology between male and female puffin parents suggest that energetic demands of chick-rearing may be greater for females, which is consistent with observations that females invest more in chick provisioning than males.

4.2 INTRODUCTION

The breeding season is the most energetically and physiologically demanding part of the annual cycle for long-lived seabirds; therefore, they breed conservatively to maximize their long-term survival and future reproductive success (Drent & Daan 1980, Breuner 2003, Bókony et al. 2009). Balancing the costs of parental care requires trade-offs between self-maintenance and chick provisioning, as foraging for food is a costly activity for chick-rearing parents (Erikstad et al. 1997, Weimerskirch et al. 1997). Flexible foraging strategies are necessary for seabird parents, as prey availability surrounding breeding colonies is widely and unpredictably distributed. Focusing on alternate prey species (Burger & Piatt 1990, Baillie & Jones 2003, Burke & Montevecchi 2008, Eilertsen et al. 2008), adjusting provisioning effort (Tveraa et al. 1998, Wernham & Bryant 1998, Takahashi et al. 1999b, Weimerskirch et al. 2001), or completely abandoning breeding in the poorest foraging conditions (Johnsen et al. 1994, Erikstad et al. 1997, 1998, 2009) are different strategies by which parents can balance their own survival with reproductive success.

Since the energy demands of foraging are challenging, biparental care is necessary for most seabird species (Ligon 1999). Both sexes often invest equally in raising offspring, although the relative time and energy spent on each activity may differ. Sex-specific parental roles are common in seabirds and the duties performed can differ in several ways (Creelman & Storey 1991, Harding et al. 2004, Paredes et al. 2006, Bulla et al. 2014). Duties can vary according to the quality, amount and/or timing, and investment, which can change depending on the available resources. The amount or quality of

parental responsibilities can be unequal, as shown in marbled murrelet *Brachyramphus marmoratus* males that feed their chicks more often than their female partners during late chick-rearing (Bradley et al. 2002). The investment in duties may be equal, but the method may differ. Wilson storm petrel *Oceanites oceanicus* parents both provision their chicks equally, however males feed chicks more frequently whereas females provide heavier meals (Gladbach et al. 2009), demonstrating that strategies can diverge while provisioning investment remains the same. Sex differences also occur in how parents respond to chick begging, as shown in female Manx shearwaters *Puffinus puffinus* that provide larger meals to chicks that beg more, whereas male parents do not (Quillfeldt et al. 2004). For Atlantic puffins *Fratercula arctica* that raise a single chick each year (Lowther et al. 2002), overall time spent on reproductive activities appears to be equal, however the time spent on specific activities differ between males and females. Males spent more time on burrow maintenance and defence, whereas females spent more time in the burrow during incubation and have higher chick-provisioning rates (Creelman & Storey 1991). While all these activities contribute to the overall reproductive success of the pair, female puffins spend more time on activities related to direct parental care.

Fixed sex-specific roles in parental investment may work when environmental conditions are good and both parents are in good condition, but when parents are unable to fulfill their duties in chick-rearing, any or all members of the family may endure costs (Paredes et al. 2005, Beaulieu et al. 2009, Harding, Kitaysky, Hamer, et al. 2009). When the effort of one parent is less, the other partner can offset this effort with compensatory behaviour; however, compensation in partnerships is not always possible or consistent and depends on environmental conditions and individual quality (Tveraa et al. 1998,

Jones et al. 2002). Experimental studies that have handicapped one partner of a pair have demonstrated that a range of compensatory behaviour exists in seabirds. The partners of handicap Cape gannets *Morus capensis* partially compensated for their partners reduction in provisioning by increasing nest attendance and foraging frequency, with the residual costs taken on by chicks with reduced growth and survival (Bijleveld & Mullers 2009). Compensatory chick provisioning behaviour occurred in common murre *Uria aalge* when a partner was wearing a tagging location device (Wanless et al. 1988); however, chicks of handicapped thick-billed murre *Uria lomvia* parents, a similar species, were fed less and had lower mass than chicks of control parents in another study. The non-handicapped parent did not compensate, and chicks had lower mass when the handicap parent was male rather than female. Handicap females provisioned more than handicapped males, as males likely prioritized their own condition to prepare for the post-fledging parental care of the chick at sea (Jacobs et al. 2013). Compensation is more difficult when food availability is poor and self-maintenance takes priority over parental investment. When no compensatory behaviour occurs, both the parent and offspring may endure physiological costs as a result.

When parental effort differs among individuals, it is expected that there will also be some variation in physiology. Corticosterone (CORT), the primary glucocorticoid in birds (Holmes & Phillips 1976), can vary with the circumstances they encounter by mobilizing energy stores and adjusting behaviour appropriately (Landys et al. 2006). High CORT levels are often associated with reduced fitness, with individuals having poor body condition or low reproductive success (CORT-fitness hypothesis, Bonier et al. 2009). For example, high CORT levels in common murre was associated with decreased

reproductive performance in hatching, fledging, and overall productivity (Kitaysky et al. 2007). When individuals encounter challenges that could be detrimental to their own survival, increasing CORT levels may redirect their energy away from reproduction and towards self-maintenance (Angelier et al. 2007). Alternatively, high CORT levels can also stimulate foraging effort when challenges arise, facilitating chick provisioning (Kitaysky et al. 1999, Doody et al. 2008, Barrett et al. 2015). During challenging situations or environments, higher CORT levels in individuals in good body condition can stimulate them to forage more thus allowing them to maintain allocation of resources to reproduction (CORT-adaptation hypothesis, Bonier et al. 2009). Female Tree swallows *Tachycineta bicolor* with enlarged broods had higher CORT levels and higher chick provisioning and fledging rates than females with reduced broods (Bonier et al. 2011). Within-individual CORT levels of common murre parents were higher in years when peak prey availability did not coincide with chick hatching compared to years when prey availability and timing of hatching matched. In addition, parents with higher CORT levels had higher provisioning rates compared to parents with lower CORT levels during a mismatched year (Doody et al. 2008). For puffins, CORT levels were higher in tufted puffins *Fratercula cirrhata* during chick-rearing when both foraging and productivity were poor, supporting the CORT-fitness hypothesis (Williams et al. 2007). Conversely, CORT levels in Atlantic puffins did not differ when foraging conditions varied between years (Rector et al. 2012). In both species, CORT levels diminished throughout the breeding stages, suggesting that puffins may be more likely to suppress CORT levels when the breeding season is lengthy, and there is a possibility the foraging conditions could improve. When challenges arise, and resource availability is poor, spatial and

temporal factors as well as the ability to improve the situation all contribute to an individual's CORT response (Rich & Romero 2005).

Haematocrit levels, measured as the relative volume of red blood cells in the total blood volume, are often used as a measure to assess the health of individuals. However, using haematocrit levels as an indicator of condition is complicated and multiple factors, including age and parasite load, can limit its use in assessing condition (Fair et al. 2007). In seabirds, haematocrit levels can indicate the aerobic condition of an individual as it relates to flying and diving performance (Elliott et al. 2010). For example, haematocrit levels of Macaroni penguins *Eudyptes chrysolophus* are positively correlated with diving performance and habitat selection, indicating that individuals with higher haematocrit levels have better foraging performance (Crossin et al. 2015). If foraging conditions are poor, deeper and longer dives may be necessary to reach available food. Slow-moving capelin were shown to aggregate in colder waters (Hedd et al. 2009), and common murrens had higher hematocrit levels during poor foraging years (Storey et al. 2017), suggesting that deep diving may be necessary to reach available prey.

Beta-hydroxybutyrate (BUTY), a plasma metabolite and primary ketone body in organisms, provides useful information about fuel utilization (Cherel et al. 1988). High BUTY levels are indicators of lipid catabolism and glucose shortage, which occurs during lipid mobilization when an organism is fasting or starving. Higher BUTY levels are expected in birds during migration (Guglielmo et al. 2005), prolonged periods of incubation (Robin et al. 1998, Bentzen et al. 2008), or during food shortages (Gannes et al. 2001). There are three phases of lipid mobilization that involve different uses of nutrients: Phase I, during early stages of lipid mobilization with rapid mass loss and lower

BUTY levels; Phase II, characterized by gradual mass loss and higher BUTY levels; and Phase III, late stage lipid mobilization characterized by rapid mass loss and lower BUTY levels (Cherel et al. 1988, Totzke et al. 1999). Parents are in Phase I when food resources are good, and parents are balancing feeding themselves and their chicks simultaneously. However, when food resources are or become poor, the conflicting demands of self-maintenance and chick provisioning likely advance parents into Phase II.

Provisioning effort of parents can be experimentally manipulated to measure whether there are differences in physiological condition due to sex differences in investment roles. Provisioning effort can be experimentally increased by prolonging the chick-rearing period to measure how much extra effort parents can exhibit. Offspring receive less or limited food when younger chicks are substituted for older ones (Johnsen et al. 1994, Bertram et al. 1996, Erikstad et al. 1997, 2009) or one or both parents are handicapped (Beaulieu et al. 2009, Harding, Kitaysky, Hall, et al. 2009, Harding, Kitaysky, Hamer, et al. 2009, Jacobs et al. 2013). In contrast, supplemental feeding studies aim to decrease parental effort and measure how parents respond when provisioning effort is potentially reduced (Hudson 1979, Wehle 1983, Erikstad et al. 1998, Takahashi et al. 1999a, Harding et al. 2002). Supplemental feeding can lessen the amount of effort parents need to provide, and/or can improve offspring condition. Previous puffin studies have shown that food-supplemented chicks typically do not gain more mass than control chicks because parents adjust their provisioning rates to align with the compensated food (Cook & Hamer 1997, Wernham & Bryant 1998, Gjerdrum 2004, Dahl et al. 2005). Since prey availability for the current colony has been generally poor though, food-supplemented chicks gained more mass than control chicks (see

Chapter 2 or Fitzsimmons et al. 2017), as parents likely did not reduce their provisioning effort because chicks were still hungry. However, food-supplementation may have reduced provisioning effort to some degree, which can be measured by a difference in parental condition between experimental groups.

Measures of physiology can indicate the energetic costs associated with parental investment and will differ if sex-specific roles emerge. If females provision their chicks at a higher rate than males (as in Creelman & Storey 1991 and Chapter 3), especially when prey availability is limited, I predict that (1) females will have higher CORT, BUTY and haematocrit levels and lower relative mass than males; (2) female condition will better predict chick growth than male condition; and (3) parent condition will be better in parents of food-supplemented chicks compared to control chicks, as the provisioning effort of the former should be reduced.

4.3 METHODS

4.3.1 Study Site

This study was conducted on Gull Island, in the Witless Bay Ecological Reserve, Newfoundland and Labrador, Canada (47°15' N, 52°46' W) during July and August 2010 through 2013. The entire reserve supports an estimated 300,000 breeding pairs of Atlantic puffins, with more than 140,000 pairs breeding on Gull Island (Robertson et al. 2004, Wilhelm et al. 2015).

4.3.2 Chick Mass and Experimental Feeding Group

Chicks were part of an experimental supplemental feeding study for one week during 2010 and two weeks during 2011 through 2013. Chicks were fed, in addition to the food provided by parents, one capelin (2010, N=25, ~15g/day) or two capelin (2011-2013, N=65, ~30g/day) or were part of an unfed control group (N=79, undisturbed or disturbed by placing a hand in the burrow). Chicks were weighed using a 500g-pesola scale at the beginning and end of the experiment to derive a measure of daily growth. See Fitzsimmons et al. (2017; Chapter 2) for further details of the experiment and method.

4.3.3 Year Differences

Due to yearly differences in capelin availability, year was factored into the analysis to take into consideration both natural and experimental feeding conditions. See previous studies for assessment methods for capelin availability for this colony (Doody et al. 2008, Regular et al. 2008, 2014, Wilhelm et al. 2008, Rector et al. 2012, Fitzsimmons et al. 2017). Capelin availability was poor in 2010 and 2011 (in addition to severe cold and wet weather in 2011, which contributed to high chick mortality), and was good in 2012 and 2013 (although hatch dates were on average much later than peak spawning activity in 2013, generating a resource/breeding mismatch during early and late chick-rearing, Table 4.1).

Table 4.1 Mean chick hatch dates (chick-rearing period of 38-44 days), and capelin abundance and spawning information, to indicate a greater match between resources and chick rearing in the year 2012 compared to the other years

Year	Mean chick hatch dates	Peak capelin spawning dates	Capelin spawning activity period	Offshore capelin abundance indices
2010	July 1	July 11	June 26-July 20	Low
2011	July 1	July 5	June 26-July 20	Medium
2012	June 30	July 14	June 15-August 12	Medium
2013	July 9	July 3 & 22	June 16-July 8 & July 22-24	High

4.3.4 Adult Condition

Adult Atlantic puffins (N=113) were caught after the chick experiment had concluded, during the first two weeks in August when chicks were approximately 30-40 days old (1-2 weeks pre-fledge). Not all parents of chicks in the experiment were caught. Adults were captured while in their burrow at night (between 21:00 and 3:00 hours). Individuals were placed in a cloth bag, with blood samples taken within three to five minutes of first touching the bird, and all birds were placed back in their burrow within fifteen minutes. Individuals were weighed using a 1000g Pesola and banded with a USFWS metal band.

Blood was collected for measuring corticosterone (CORT) levels, beta hydroxybutyrate (BUTY) levels, haematocrit levels and for determining sex. Approximately 2 ml of blood was taken from the brachial vein using a 23 or 25-gauge

butterfly needle, in which .5 ml was collected using blood spot cards (Whatman, GE Healthcare Life Sciences) and the remaining blood was stored in a 2 ml vial. Blood spot cards were dried for at least 24 hours and were stored in plastic bags until the end of the field season, then transferred to a -20-degree Celsius freezer for storage. Whole blood was spun for 10min at 2200 x g using a mini centrifuge (Fisher Scientific, Ottawa ON) in the field within an hour of collection and serum was separated from the red blood cells. Both were stored separately, and samples were either taken off the island within 12 hours to be frozen or were frozen on site, both kept in a -20-degree Celsius freezer until analysis.

4.3.5 Body Mass

Body mass of adults was used as an index of body condition, as this has been used in several other studies measuring condition in alcids (rhinoceros auklets *Cerorhinca monocerata*; Niizuma et al. 2002; thick-billed murres, Gaston & Hipfner 2006; Atlantic puffins, Rector et al. 2012; common murres, Storey et al. 2017). Using an index of body condition (residuals of mass regressed on the first principal component of wing, tarsus, and culmen), a difference was found between the sexes in tufted puffins (Williams et al. 2007). However, using this same index yielded a high correlation with body mass ($r = .893$) for our Atlantic puffins and the overall results remained the same. Therefore, body mass was used as the condition measure.

4.3.6 BUTY Levels

Serum samples were analysed for BUTY concentrations using a microplate spectrophotometer (Biotech Powerwave XS, Fisher Scientific, Nipean ON) and a kinetic end-point assay using a D-3-Hydroxybutyric acid Colorimetric assay kit (E0907979 from R-Biopharm, Marshall, Michigan) with linearity standards (Stanbio Laboratories, Boerne, TX, USA) following the protocol of Guglielmo et al. (2002, 2005).

4.3.7 Haematocrit Levels

Blood was collected in heparinized capillary tubes (Fisher Scientific, Ottawa, ON) that were sealed at one end using Critoseal® (Fisher Scientific, Ottawa, ON). Capillary tubes were spun for 10min at 2200 x g using a Galaxy 7D VWR centrifuge (VWR, Edmonton AB). The haematocrit percentage was calculated for each capillary tube by the length of section containing red blood cells divided by the length of the total sample, as measured with a ruler to the nearest millimetre.

4.3.8 CORT Levels

CORT concentrations were determined using COAT-A-COUNT Rat CORT ¹²⁵I radioimmunoassay kits (Cat. #TKRC1, InterMedico, Markham, Ontario) with modifications for measurements using blood spot cards (see Doody et al. 2008, Rector et al. 2012 for validation and procedure). This assay has a 2.9% cross-reactivity with 11-deoxycorticosterone and less than one percent cross-reactivity with other steroids,

including progesterone. Blood spots were used because of their greater convenience in the field and because they retain higher hormone levels than long-stored serum samples (Rector et al. 2012). Intra-assay CVs were 5.50-5.89% and inter-assay CVs were 9.5-17.2%. Assay values were adjusted relative to a pooled sample used in all assays for between-year comparisons to standardize CORT values; however, analyses on the non-adjusted CORT values yielded the same overall results. Blood spot CORT values were converted to serum values of ng.ml^{-1} (using the equation described and validated in Rector et al. 2012) when reported in the tables/figures to allow for comparisons to CORT values in other studies.

4.3.9 Sex Determination

DNA was extracted from either blood spot cards or red blood cells using a DNeasy Blood and Tissue Kit (Qiagen). Sex was determined using a CHD (chromodomain helicase DNA)-based molecular method (Dawson et al. 2001) using highly conserved primers 2550F and 2718R. Females were characterized by two fragments (CHD1W and CHD1Z) and males were characterized by one fragment (CHD1Z) following polymerase chain reaction and agarose electrophoresis.

4.3.10 Statistical Analyses

The effects of year, sex, and experimental feeding group on body mass, haematocrit, BUTY and CORT levels were analyzed using separate univariate General Linear Models. Significant main effects were analysed using Tukey HSD post-hoc comparisons and significant interactions were deconstructed with one-way ANOVAs and

t-tests. Tests of normality (Shapiro-Wilk test) for CORT and BUTY values were significant, indicating that these values were not normally distributed; therefore, CORT and BUTY values were log transformed for all analyses.

Linear forward stepwise regressions were used to identify the adult physiological variables that best explained chick growth and Pearson correlations examined relationships between these variables. Means are expressed as ± 1 SE. All comparisons are two-tailed, and differences were considered significant when $p < 0.05$. All statistical analyses were performed using SPSS, version 23.0 (IBM, Armonk, NY, USA).

4.4 RESULTS

4.4.1 Body Mass

There was a significant interaction of feeding group and sex on mass, $F_{1,97} = 4.04$, $p = 0.047$, with females weighing less than males among parents of control chicks, $t_{56} = 4.23$, $p = 0.001$ (Table 4.2). There was no sex difference in mass between male and female parents of food-supplemented chicks and there was no significant difference in mass between years or feeding groups.

Table 4.2 Mass (g, mean \pm SE) of male and female Atlantic puffin parents with food-supplemented or control chicks, indicating that female parents were of relatively less mass than male parents of control chicks (bold values indicate significant differences at $p < 0.05$)

Experimental Group	Male	N	Female	N
Control	454 \pm 4	31	421 \pm 7	27
Food-Supplemented	442 \pm 5	35	433 \pm 6	20

4.4.2 BUTY Levels

There was a significant interaction of feeding group and sex on BUTY levels, $F_{1,86} = 5.60$, $p = 0.020$, showing that female parents of food-supplemented chicks had lower BUTY levels than female parents of control chicks (Table 4.3). There was a significant effect of year with parents having lower BUTY levels in 2011 compared to 2012 and 2013, $F_{3,86} = 5.17$, $p = 0.002$ (Table 4.4). No other main effects or interactions were significant.

Table 4.3 Mean \pm SE of BUTY levels (mmol.L^{-1}) of male and female Atlantic puffin parents with food-supplemented or control chicks, indicating that female parents of control chicks had higher BUTY levels than female parents of food-supplemented chicks (bold values indicate significant differences at $p < .05$)

Experimental Group	Male	N	Female	N
Control	0.63 \pm 0.03	29	0.76 \pm 0.07	24
Food-Supplemented	0.68 \pm 0.03	33	0.60 \pm 0.04	16

Table 4.4 Mean \pm SE (N) differences in CORT levels (ng.ml⁻¹), BUTY levels (mmol.L⁻¹), and haematocrit (% RBC) of Atlantic puffin parents by year (*a* is significantly different than *b* at $p < 0.05$)

	2010	2011	2012	2013
CORT (ng.ml ⁻¹)	22.36 \pm 3.07 (30)	31.98 \pm 3.95 (24)	27.86 \pm 3.07 (28)	20.79 \pm 2.13 (26)
BUTY (mmol.L ⁻¹)	0.67 \pm 0.05 (28)	0.55 \pm 0.04 (19) ^a	0.74 \pm 0.02 (29) ^b	0.69 \pm 0.05 (26) ^b
Haematocrit (%)	61 \pm 2 (28) ^b	62 \pm 1 (18) ^b	58 \pm 1 (19)	56 \pm 1 (20) ^a

4.4.3 Haematocrit Levels

Parents had lower haematocrit levels in 2013 compared to 2011 and 2010, $F_{3,69} = 4.73$, $p = 0.005$ (Table 4.4). There were no significant differences between haematocrit levels in 2012 or any other year. There were no significant differences in haematocrit levels between sexes or feeding groups or interactions between these variables.

4.4.4 CORT Levels

There were no significant main effects or interactions of sex, feeding group or year on parental CORT levels (Table 4.4). The only significant relationship between any of the physiological variables was a weak but significant negative correlation between CORT levels and adult mass, $t_{106} = -2.14$, $p = 0.035$, $r = -0.20$ (Figure 4.1).

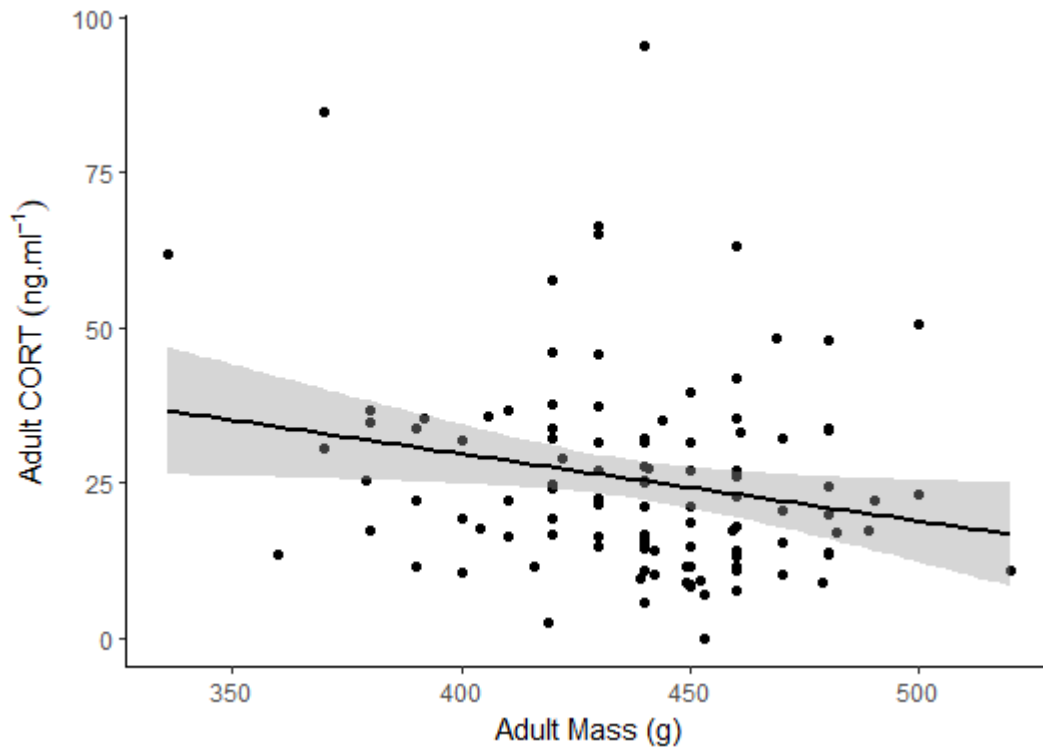


Figure 4.1 Mean and 95% confidence intervals, indicating Atlantic puffin parents with higher CORT levels (ng.ml^{-1}) have lower mass (g)

4.4.5 Chick Growth

Physiological indicators of parental condition were analyzed (CORT, BUTY and mass of males and females) to see if any explained chick growth. The only significant predictor of chick growth across all years was female BUTY levels, $F_{1,30} = 12.42$, $p = 0.001$, $r = -0.55$, $r^2 = 0.30$ (Figure 4.2), indicating that lower chick daily mass gain was associated with higher BUTY levels. The only significant predictor of chick growth in a single year was adult mass in 2011, $F_{1,12} = 6.32$, $p = 0.027$, $r = 0.61$, $r^2 = 0.38$, indicating that adults with higher mass had chicks with greater daily mass gain (Figure 4.3). No

other adult physiological measure predicted chick growth in any other year or between feeding groups.

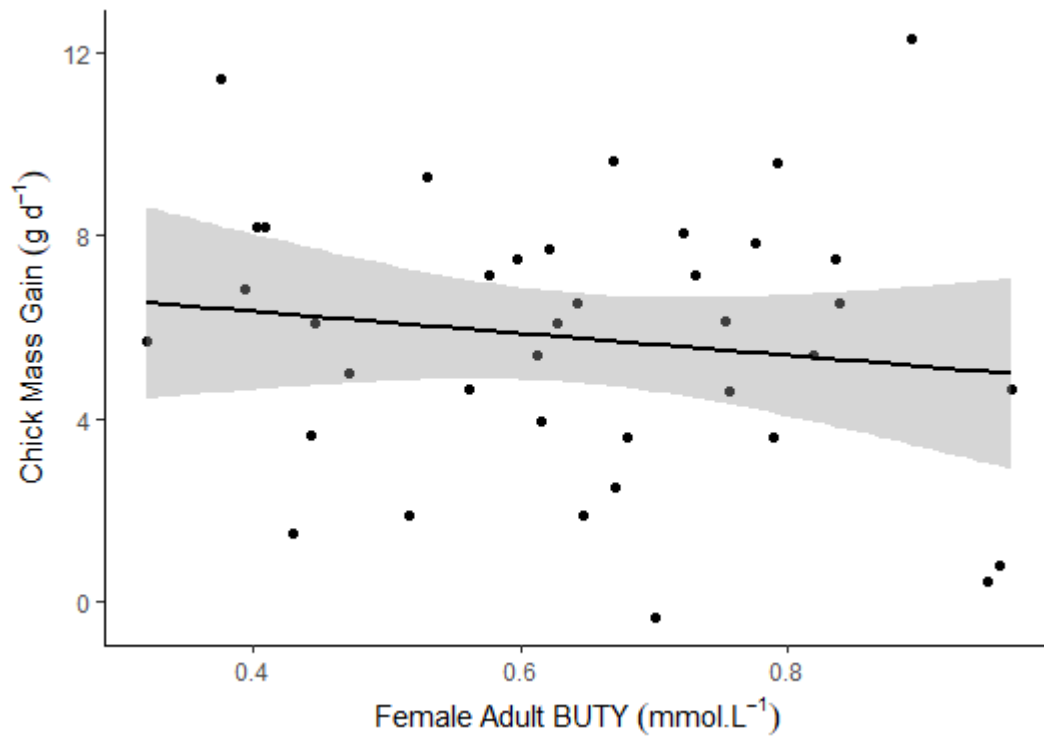


Figure 4.2 Mean and 95% confidence intervals, indicating daily mass gain (g) of Atlantic puffin chicks is best explained by BUTY levels (mmol.L⁻¹) of female parents. Female parents with higher BUTY levels have chicks with lower daily mass gain

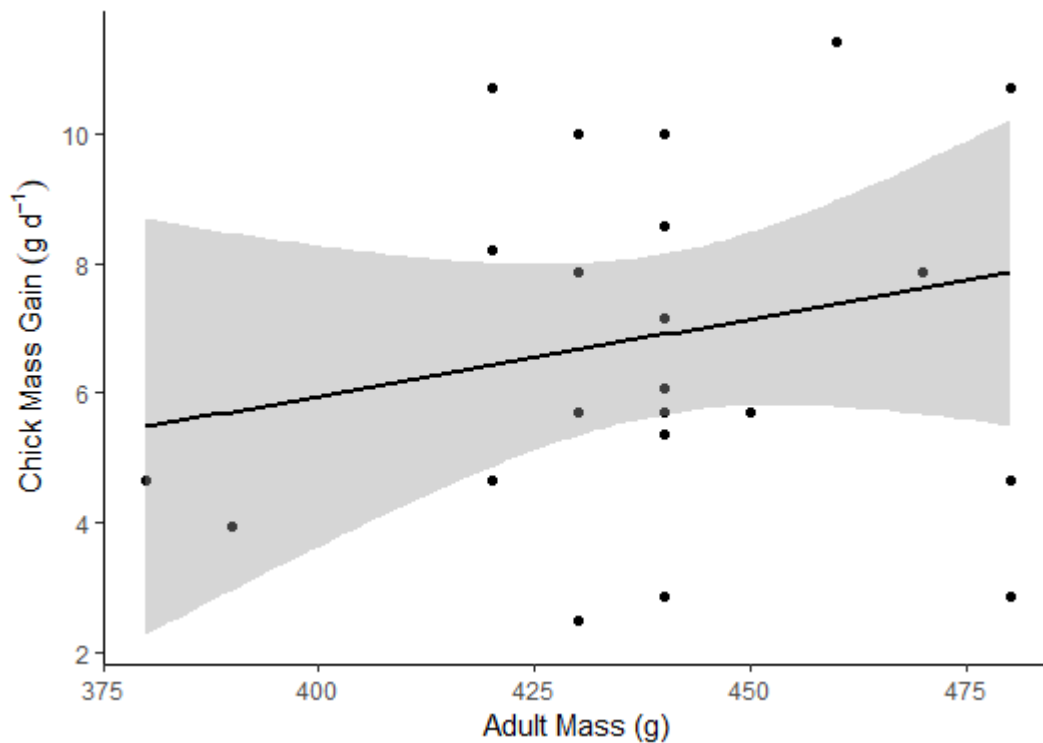


Figure 4.3 Mean and 95% confidence intervals, indicating that in the poor foraging year of 2011, daily mass gain (g) of Atlantic puffin chicks is best explained by adult mass (g). Adults with greater mass have chicks with higher daily mass gain

4.5 DISCUSSION

Female parents of control chicks weighed less than males whereas the mass of male and female parents of food-supplemented chicks did not differ. Female parents of control chicks had higher BUTY levels than female parents of food-supplemented chicks and the only significant predictor of higher chick growth overall was low BUTY levels in female parents. Parental mass best explained chick growth in 2011 but not in other years. There were no differences in CORT levels among years, or between parents or feeding groups;

however, parent mass was negatively correlated with CORT levels. In summary, food availability affects physiological condition of males and females differently.

Food availability during the years of this study were poor in 2010 and 2011 and good in 2012 and 2013 (see Doody et al. 2008, Regular et al. 2008, Wilhelm et al. 2008, Rector et al. 2012, Fitzsimmons et al. 2017, Storey et al. 2017 for greater details of foraging conditions in Witless Bay). In addition to poor foraging conditions in 2011, weather conditions were also wetter and colder than historical weather conditions. In 2013, there were bimodal peaks of capelin spawning during early and late chick rearing, with poor capelin availability during mid chick rearing. Relative to each other, the foraging conditions during the years in this study varied from good to poor. However, the overall food resources for seabirds in the Witless Bay region have deteriorated over the past several decades. Abundance has declined and there is greater variation in the timing of capelin spawning, providing more difficult conditions for parents to find food for their chicks during chick-rearing (Regular et al. 2014, DFO 2015, Fitzsimmons et al. 2017). Poor food availability near seabird colonies requires longer foraging trips and more searching for available fish, requiring greater energy expenditure (Harding et al. 2013).

Even when prey sources are good, biparental care is necessary for puffins to successfully rear a single chick each season (Lowther et al. 2002, Harris & Wanless 2011). Male and female puffins are monomorphic, and although females are on average slightly smaller in size (Lowther et al. 2002), the greater difference in mass between parents of control compared to food-supplemented chicks suggests that food supplementation provided to chicks predominantly benefited female parents. In addition, higher BUTY levels in females of control compared to food-supplemented chicks

suggests that food supplementation reduced female provisioning effort. If female parents provision chicks more than males (as suggested by Creelman & Storey 1991 and Chapter 1), food-supplementation to chicks would provide females more opportunity for self-feeding, as chick-provisioning demands would be less.

BUTY measurements, useful for estimating lipid catabolism in birds (Cherel et al. 1988, Jenni-Eiermann & Jenni 1994), can be detected in short-term fasting of single day mass changes (Anteau & Afton 2008) or long-term fasting over a week (Dietz et al. 2009). BUTY levels have been negatively correlated with mass (Jenni-Eiermann & Jenni 1994, Williams et al. 1999, Anteau & Afton 2008, Dietz et al. 2009) and studies often measure BUTY levels in birds to detect habitat and foraging quality (Guglielmo et al. 2002, 2005). Across all years, female BUTY levels significantly predicted chick growth, with low chick mass relating to high BUTY levels in females. This is consistent with higher BUTY levels in female parents of control chicks, which have lower mass, and lower BUTY levels in female parents of food-supplemented chicks, which have higher mass. Higher BUTY levels may be related to females investing relatively more effort than males in finding food for their chicks than themselves. With less than ideal foraging conditions though, finding food may not be that successful.

The significantly lower BUTY levels in 2011 during the poorest foraging year were likely a result of parents already having lost acceptable mass levels and having burned off lipid reserves as in Phase III, late stage lipid mobilization. Low BUTY levels in years of poor foraging correspond with findings of lower BUTY levels in common murres during poor foraging years, which may have already lost acceptable mass levels by the time of capture (Storey et al. 2017). 2011 was also complicated by cold and wet environmental

conditions, leading to a high mortality rate of chicks (see Chapter 3). It was only in 2011 that chick growth was best explained by parent condition, with high parental mass relating to high chick mass. As measurements were taken late in chick-rearing, only parents in good condition and with delayed mass loss would have been able to maintain raising chicks to this developmental stage and would be best able to provide sufficient food even with the poor environmental conditions.

Due to the variety of interacting factors that can affect haematocrit levels, haematocrit is limited in its value as an indicator of condition in birds (Fair et al. 2007). Although haematocrit levels were significantly lower in 2013 compared to 2010 and 2011, haematocrit levels of puffins in this colony across all years were within the range previously reported for this species (Wanless et al. 1997, $57.9 \pm 9.3\%$). If higher haematocrit levels are related to longer and deeper dives, which may be necessary to reach capelin in poorer foraging years, it would support the findings of higher haematocrit levels in the poor years, 2010 and 2011, compared to the better years, 2012 (although non-significant) and 2013, an intermittent season of capelin availability with a high abundance of capelin late in chick-rearing when adults were captured.

There were no differences in CORT levels between years or feeding groups, and only a weak significant negative relationship with higher CORT levels in parents with lower mass. With measurements taken late into chick-rearing, it is possible that CORT levels may have declined throughout the season (as in common murre, Storey et al. 2017) or that elevated CORT does not mediate foraging challenges for puffins. Although other seabirds show elevated CORT levels during poor foraging conditions (Kitaysky et al. 1999, Doody et al. 2008, Barrett et al. 2015), Atlantic puffins have a lengthy chick-

rearing season that may allow them to suppress elevations in CORT levels during poor foraging conditions in the chance that food availability may improve (Rector et al. 2012). Females had overall higher CORT levels than males in Rector et al. (2012), which is contrary to the findings in this study of no sex differences between CORT levels of parents. In the Rector et al. (2012) study, CORT levels were elevated in females when all stages of the breeding season were analysed together, however, there was no significant CORT elevation during any one breeding stage. The present study only measured CORT during the chick-rearing stage, which suggests that breeding costs for females may be cumulative over the entire breeding season.

Overall results suggest that reproductive costs during chick rearing are higher for female than male puffins in this colony. When local food resources constrain reproductive performance, prioritizing self-maintenance over parental investment corresponds to more conservative reproductive strategies (Drent & Daan 1980, Bókonyi et al. 2009). Although long-lived seabirds tend to favour long-term survival over immediate parental investment, especially when resources are limited, female parents may not always adhere to this conservative breeding strategy. Greater physiological demand is placed on females during early reproduction with egg-laying, and this may carry-over throughout incubation and chick-rearing, leaving females in poorer physiological condition than males (Heaney & Monaghan 1995, Monaghan et al. 1998, Bauch et al. 2010). If food conditions are poor, recovering from this energetic demand may be challenging. Puffins in Scotland that had supplemental fed chicks in one year had greater fledging success in the following year and were also more likely to return to breed (Wernham and Bryant 1998). Alternatively, greater investment by females early in reproduction through egg laying may also increase

their overall investment input. Females may have a higher threshold than males for deciding when to invest more in self-maintenance for future long-term survival than in current parental care.

Due to the high environmental variability to which puffins are exposed to throughout their life, their ability to adjust breeding effort is necessary for long-term survival. Enduring greater physiological costs for reproductive success may be possible for females in the short-term. However, successive breeding attempts in years with poor environmental conditions may lead to long-term detrimental consequences.

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CHAPTER 5 - BEGGING THE QUESTION: HOW DO CHANGING FOOD RESOURCES AFFECT PUFFIN CHICK BEHAVIOUR AND GROWTH?

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5.1 ABSTRACT

Atlantic puffins *Fratercula arctica*, like many long-lived seabirds, adopt a conservative breeding strategy that maximizes their own fitness, especially when environmental conditions are poor. However, parent-offspring conflict arises over the amount of provisioning effort a parent provides and begging from chicks may influence parental provisioning. An experimental food supplementation study was conducted in two breeding seasons that differed in prey availability. Observations included 2464 hours of infra-red video recordings from 14 burrows, with each burrow filmed over a 12-day period. Chicks produced two separate calls, one being a screech call that appears to signal hunger level and the other is the peep call which indicates chick quality. Similar to other studies, the proportion of visits with screech calls was higher in no-food visits compared to food visits. After food supplementation, the proportion of screech calls was reduced in food visits, but not in no-food visits. Contrary to predictions, the proportion of screech calls during no-food visits was not lower in the good compared to poor foraging year. Whether or not the chick screeched did not influence the time between parent visits returning with food. Male parents took longer to return to feed their female chicks than did female parents. Male and female parents did not differ in the time intervals between feeds to male chicks. Male chicks gained more mass than female chicks during the experimental study period, however both males and females were provided the same amount of food, suggesting other factors may influence mass gain. Although screech begging calls do provide information to parents on their chick's hunger levels, begging calls may be used more as a cumulative indicator of chick nutritional status.

5.2 INTRODUCTION

Parent-offspring conflict over the optimum level of care for offspring is common, as both parents and offspring are selected to maximize fitness. Although there is some cooperation due to the high relatedness between them, parents need to balance investing in their current reproductive effort with self-maintenance, to be able to invest in future offspring. Therefore, conflict can arise between parents and offspring as to the amount of investment parents provide (Hamilton 1964, Trivers 1974). Foraging is energetically demanding for parents. In order to maximize their own fitness, parents will expend energy to provision their offspring as needed to successfully fledge, but offspring may demand more and hence conflict develops (Godfray 1991).

There is some variability in the amount of control parents and offspring have over the decisions involved in parental investment. Avian offspring exert control primarily by using solicitation signals to convey their food requirements. Leach's storm petrel *Oceanodroma leucorhoa* parents increased provisioning frequency based on chick begging when the second parent was absent and decreased provisioning when chicks were provided supplemental food. However, when a parent was removed, increased provisioning by single parents did not exceed the parents' ability to maintain their own body condition, and chicks weighed less overall than control chicks (Takahashi et al. 1999). These results suggest that both offspring and parents had an influence on parental investment. However, parents of Manx shearwater *Puffinus puffinus* foster chicks that were younger than their own chick did not respond to begging in late chick-rearing when chicks would normally fledge (Riou et al. 2012). Parent-offspring theory predicts that

conflict is greatest when parents are withdrawing investment near fledging, and these studies demonstrate that parents can be influenced by chick begging, but parents exert final control over investment, especially as investment decreases close to fledging (Riou et al. 2012, Trivers 1974).

Solicitation signals may be necessary to convey an offspring's condition that is otherwise cryptic (Godfray 1991). For solicitation signals to be evolutionarily stable, they should be costly and indicate nutritional status as cost-free signals could become dishonest. For example, captive canary *Serinus canaria* nestlings were not fed for a period of time to induce begging, and then provided supplemental food that mimicked normal provisioning amounts from parents. Chicks that begged for a longer period of time before being fed incurred growth costs as they gained less mass than chicks that begged for a shorter period of time but were fed the same amount (Kilner 2001). These results indicate that chicks will incur growth costs if chicks have to expend more energy begging and parents do not respond to solicitation signals with food.

Burrow-nesting birds often use begging calls to solicit food as it eliminates the need for visual cues about chick condition. Two separate studies on thin-billed prions *Pachyptila belcheri* found that parents increased provisioning with increased chick begging, which resulted in decreased adult body condition (Quillfeldt et al. 2006, Duckworth et al. 2009). Wilson's storm-petrel *Oceanites oceanicus* chicks in poor body condition begged at higher frequencies and received larger meals from parents than chicks in better condition (Gladbach et al. 2009). Multi-chick broods use begging signals to solicit food from parents by providing parents information about how to allocate food amongst the brood (MacNair & Parker 1979). Studying parental investment in multi-

chick broods is complicated by sibling competition in addition to parent-offspring conflict, whereas studying solicitation signals in single chick broods is advantageous as it eliminates any confounding conflict between competing offspring.

The Signal of Need theory is the most prominent of theories to guide signaling research in the last several decades (Godfray 1991, Wright & Leonard 2002, Mock et al. 2011), suggesting that low quality offspring should beg more to indicate poor condition to parents, and parents should consequently provide more food to that chick. The Signal of Quality theory, however, suggests that parents use signals to make decisions to feed higher quality offspring with the best potential to survive (Grafen 1990). With both the Signal of Need and Signal of Quality theories, parents control resource allocation. When foraging conditions are at the extremes of good or poor, a shift in parental provisioning responses is likely, and this change may be the key factor in whether signals are used or acted upon. It would be more important for parents in general to detect need; however, in poor foraging conditions, a parent may need to make decisions about which offspring they can realistically raise to independence. For Atlantic puffins, it was demonstrated that chicks were able to both signal need and quality, using two distinct begging calls (Rector et al. 2014). Chicks in better body condition emitted peep calls more frequently than chicks in poor body condition with lower growth rates, demonstrating a signal of quality. Screech begging calls, a signal of need, were more common during parental visits with no food and decreased in frequency once chicks were food supplemented. In the current study, I focus on screech begging calls in Atlantic puffin chicks and whether they use screeches as a signal of need. In contrast to puffins that bring back fully intact fish to their chicks, Procellariiform (such as storm petrels) parents provision their chicks by

regurgitating food. Begging by Procellariiforms species can indicate to parents their level of hunger and parents can respond by regurgitating food in varying meal sizes (Ricklefs 1990). In contrast, if puffin chicks vocalize to parents to indicate their level of hunger during a visit without food, parents can only respond by leaving the burrow to forage and return with food. Therefore, in puffins, it is not the begging call vocalized during the visit that may influence the parental decision to provision, but instead the begging calls produced during the previous visit by the same parent.

Offspring sex may influence differential allocation of resources from parents, especially in sexually size-dimorphic species (Wojczulanis-Jakubas et al. 2013). However, in minimally size-dimorphic species, factors other than size may influence why one sex may be more energetically costly to raise than the other, as they provide greater fitness returns. For example, food supplemented black-legged kittiwake *Rissa tridactyla* parents reared equal numbers of male and female offspring, while unfed parents reared more female chicks. Male kittiwakes are more costly to rear as they are on average slightly larger and compete for nesting sites prior to breeding (Merkling et al. 2012).

Sex differences in reproductive behavioural roles may also contribute to different development costs. For example, provisioning rates of common murre *Uria aalge* parents from two different colonies differed in which offspring sex was costlier to raise. In a Newfoundland, Canada colony, parents fed male chicks more than female chicks, presumably because males have the additional parental care of post-fledged chicks and spend more time in the colony during the pre-lay period. Therefore male chicks would be costlier to raise, as they have a greater fitness value (Cameron-MacMillan et al. 2007). In a colony in Hornøya, Norway, common murre parents preferentially fed female chicks.

While males also have post-fledging care of their chicks, females also have an additional role defending the nesting site for weeks after the breeding season has ended, and in the case of the murre colony in Hornøya, there has been a 5-fold increase in population size, leading to greater competition for quality nesting areas (Kristensen et al. 2013). As for puffins, adult males are on average slightly larger than females, but some females can be larger than males within pairs (range of 4-27%; Bond et al. 2016). As male and female puffins are relatively the same size, this would imply that there should be little to no cost differences in rearing female versus male chicks. There are some behavioural (Creelman & Storey 1991; Chapter 3) and physiological (Rector et al. 2012; Chapter 4) differences between male and female puffin adults. However, there is no literature that suggests that offspring of one sex should be preferentially produced or cared for over the other, especially when environmental conditions are poor.

As found in Rector et al. (2014), I predict that the results in this study will replicate the findings that there will be a higher proportion of screech call visits compared to peep call visits when parents do not bring food, and a lower proportion of screech call visits compared to peep call visits when parents do bring food. In addition, I predict that screech calls during visits will be reduced after supplemental feeding. Expanding on the Rector et al. (2014) results, I predict that 1) there will be fewer visits with screech calls during the good compared to the poor foraging year; 2) individual parents will make visits with food more quickly after chicks produce screech calls and 3) the amount of food provided to male and female chicks will not differ.

5.3 METHODS

5.3.1 Study Site

The study was conducted on Gull Island in the Witless Bay Ecological Reserve, Newfoundland and Labrador, Canada (47°15' N, 52°46' W) during May to August 2011 and 2012. The entire reserve supports an estimated 300,000 breeding pairs of Atlantic puffins *Fratercula arctica*, with more than 140,000 pairs breeding on Gull Island (Robertson et al. 2004, Wilhelm et al. 2015).

5.3.2 Experiment

Chicks were selected for the study when they were at least 10 days old at the beginning of the study (2011: N = 10, mean age = 15 days; 2012: N = 9, mean age = 14 days) and chicks were between 21 and 32 days at the end of the study period. The start dates for each burrow ranged from July 9 to August 1 in 2011 and July 5 to July 26 in 2012. If hatch date was unknown (2011: N = 6; 2012: N = 6), growth measurements were used to assess approximate age of the chicks, employing a technique developed at this colony that uses a regression of age on wing length of chicks of known age (2011: n = 15, $r = 0.61$, $\text{age} = .11 (\text{wing}) + 11.61$; 2012: n = 13, $r = 0.67$, $\text{age} = .13 (\text{wing}) + 8.80$; Rodway 1997). At least one adult from each burrow was captured, weighed and banded. Parents were identified as either the male or female parent by colored leg bands with a Passive Integrated Transponder (PIT) tag and were later genetically sexed. See Chapter 3 for additional details on parent identification.

Burrow scope cameras (Peep-a-Roo monochrome 1.0 diameter video probe, Sandpiper Technologies, Manteca, CA) retrofitted with omnidirectional microphones (RadioShack 33-3013) and connected to a DVR recording system (Archos AV400 Series DVR) were used to record parent–offspring interactions and chick vocalizations. Cameras were deployed in burrows for two separate 4-day periods of filming: an initial pre-supplemented period, followed by 4 days of food supplementation. These two recording periods were separated by a 4-day food supplementation period that was not recorded. Recording did not take place during the middle 4-day period to allow chicks to be acclimatized to the supplemented food and for the cameras to be used in other burrows, as the number of cameras were limited. Other than having supplemental capelin provided to chicks each day, chicks remained undisturbed for the 12-day experimental period, except for being measured at the end of each recording period. During the second measurement, a small amount of blood (0.5cc) was taken from the brachial vein for genetic sexing. Year was factored into the analysis due to differences in natural prey availability. See Chapter 2 for greater details regarding foraging conditions in the years of this study.

5.3.3 Sex Determination

Blood taken during capture was used to genetically determine sex. DNA was extracted from blood spot cards using a DNeasy Blood and Tissue Kit (Qiagen), and the sex of adults and chicks were determined using a CHD (chromodomain helicase DNA)-based molecular method through polymerase chain reactions (PCR). The PCR method used highly conserved primers 2550F and 2718R. Females were characterized by two fragments (CHD1W and CHD1Z) and males were characterized by one fragment

(CHD1Z) following agarose electrophoresis. The protocol was based on the methods in Dawson et al. (2001).

5.3.4 Video Analysis

Videos were analyzed for behaviours of 10 chicks in 2011 (6 chicks were fed one supplemental capelin and 4 chicks were fed two supplemental capelin) and 9 chicks in 2012 (6 chicks were fed two supplemental capelin and 3 chicks were fed no supplemental capelin (controls)). See Chapter 3 for greater details of experiment method. Four days of videos for each experimental period (pre-supplemented and food supplemented/control) resulted in a total of ~1760 hours in 2011 and ~1584 hours of video in 2012 that were viewed in Final Cut Pro X (v10.1 Apple Inc) and coded for a series of behaviours during parent-chick interactions. Type of visit (food or no food provided to chick), parent identity, start and end time of visit, and the type of begging vocalizations of chicks were recorded for each visit.

Consistent with Rector et al. (2014), two different begging vocalizations were identified and either classified as ‘peep’ calls (brief and rapid vocalizations repeated at regular intervals) or ‘screech’ calls (lengthy vocalizations repeated at irregular intervals; see Figure 5.1 for a spectrogram). For each visit, the chick was identified as either producing only peep calls, only screech calls, or a mix of both peep and screech calls. Since almost all visits with screech calls had at least one peep call in it, both mixed and purely screech calls were considered a ‘screech’ visit.

To estimate the total amount of nutrition provided to chicks, the amount of fish was calculated as 1 for large fish (capelin and sand lance) and 0.5 for larval fish loads. This is

a rough approximation of nutrition that assumes that larval fish loads are half the quality of capelin and sand lance loads. Total food intake included fish provisioned by parents, in addition to any supplemental food, and the total fish equivalencies are denoted as fish/day. The question addressing the amount of time between parental visits was analyzed using only the same 14 burrows used in Chapter 3, as parent identity could only be confirmed in those burrows. To measure whether begging calls influenced the return visit of parents bringing food, the time between a food visit and the previous visit was calculated, and whether or not the chick screeched during this previous visit was recorded.

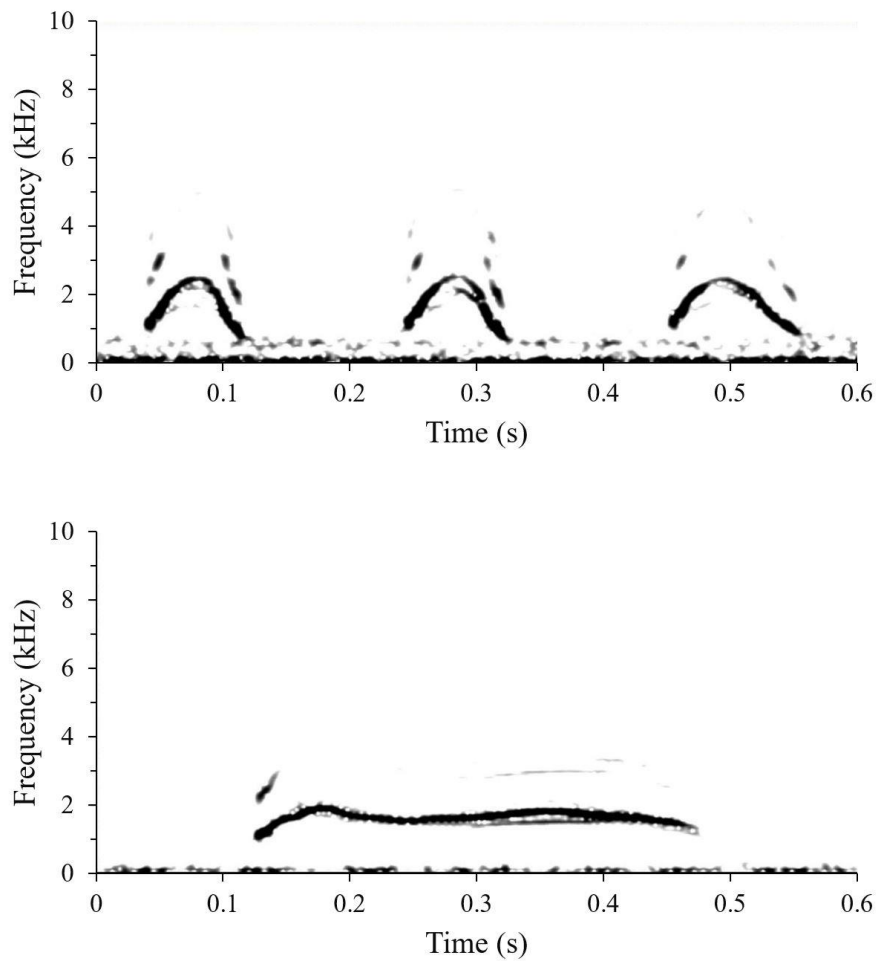


Figure 5.1 Two different vocalizations from Atlantic puffin chicks. Top spectrogram exhibits a ‘peep’ begging call, with short and repeated vocalization of an inverted U-shape. Bottom spectrogram exhibits a ‘screech’ begging call, with a longer vocalization and an uneven frequency.

5.3.5 Statistical Analysis

Differences between groups were tested using Student’s t-test or Welch’s two sample t-test for unequal variances. Wilcoxon Mann-Whitney and Wilcoxon signed-rank

tests were used to compare the change in proportions of begging calls. The effects of year, experimental period, parent sex, chick sex, previous visit type and chick begging calls on latency of time between a food visit and a subsequent visit by individual parents were determined using a generalized linear mixed model (GLMM) with maximum likelihood and a negative binomial error distribution, using the glmm TMB package (Brooks et al. 2017). The best predictors for chick mass gain were determined using a general linear model (GLM) using base R (R Core Team 2017). There was a significant difference in the total food consumed by chicks in 2011 (3.06 ± 0.24 fish/day) compared to 2012 (4.51 ± 0.59 fish/day), $t_{10.598} = 2.27$, $p = 0.045$, therefore year was factored into the analysis of differences in chick mass gain. However, including year as a factor did not significantly improve the model and was not a significant factor affecting mass gain and was therefore excluded from the final model. The final model included age, sex, and total food consumption during the experimental period, which was the duration of time between mass measurements and includes both supplemented food and food provided by parents. Control burrows were left in the analysis ($n=3$) because the calculated total amount of food included the supplemented capelin and therefore accounted for control chicks receiving less food. Chick ID was included as a random factor to account for individual differences. Means are expressed as \pm SE. All analyses were conducted in R version 3.4.2 (R Core Team 2017).

5.4 RESULTS

The proportion of visits with screech calls was significantly lower in food visits ($\chi^2_1 = 260.29$, $p < 0.001$) and significantly higher in no-food visits ($\chi^2_1 = 47.90$, $p < 0.001$) compared to the proportion of food and no-food visits with only peep calls. Screech calls occurred in a significantly higher proportion of no-food visits compared to food visits ($\chi^2_1 = 101.89$, $p < 0.001$, Figure 5.2).

For experimental chicks, the proportion of food visits with screech calls was reduced after food supplementation (Wilcoxon signed-rank test, $n = 16$, $p = 0.039$), but was not reduced during no-food visits (Wilcoxon signed-rank test, $n = 16$, $p = 0.245$). For control chicks, sample sizes were too small ($n = 3$) to conduct any meaningful analyses, however there does not appear to be any reduction in the proportion of screech calls during similar periods for either food visits or no-food visits, (Table 5.1). There was no detectable difference in the proportion of no-food visits with screech calls between the good and poor foraging year (Wilcoxon signed-rank test, $n=19$, $p = 0.549$), although there were more no-food visits, hence more screech call visits, in the good compared to the poor foraging year (see Chapter 3).

The final model that offered the best explanation for latency to next visit with food by parents included an interaction term between parent and chick sex and excluded previous visit type. This model was significantly better than the model including previous visit type and no interaction terms, $\chi^2_1 = 3.32$, $p < 0.001$. Parents returned with food more quickly in 2012 ($n = 9$), the good foraging year (358 ± 40 min), compared to the poor foraging year of 2011 ($n = 10$, 539 ± 57 min), $Z = 2.54$, $p = 0.011$. Parents ($n = 19$)

returned to feed chicks more quickly during the pre-supplemented period (376 ± 38 min) compared to the food supplemented period (539 ± 64 min), $Z = 2.23$, $p = 0.026$. There was a significant interaction between parent and chick sex, with male parents (777 ± 147 min) taking longer to return to the burrow with food between subsequent visits to feed female offspring ($n = 7$) compared to female parents (312 ± 60 min), $Z = 1.98$, $p = 0.048$ (Figure 5.3), but there was no difference in return visits with food to male chicks for either parent. Whether or not the chick screeched during the visit just prior to a food visit, however, did not significantly affect the time it took for parents to return with food, $Z = 0.80$, $p = 0.423$.

Female and male chicks were the same age at the end of the study period when final measurements were taken, (female chicks, 28 ± 2 days, $n = 7$; male chicks, 26 ± 1 days, $n = 12$), $t_{12.095} = 0.82$, $p = 0.426$. Male chicks (7.3 ± 1.4 g/d) gained more mass than female chicks (2.9 ± 0.9 g/d), $F_{(1,15)} = 4.58$, $p = 0.049$ (Figure 5.4) and older chicks gained mass more slowly than younger chicks, $F_{(1,15)} = 12.61$, $p = 0.003$, $r = -0.64$ (Figure 5.5), while total food weakly contributed to chick mass gain, $F_{(1,15)} = 3.18$, $p = 0.095$. The amount of food received by chicks during the food supplementation period did not differ between male (3.82 ± 0.39 fish/d) and female chicks (3.73 ± 0.67 fish/d), $t_{10.212} = 0.12$, $p = 0.909$.

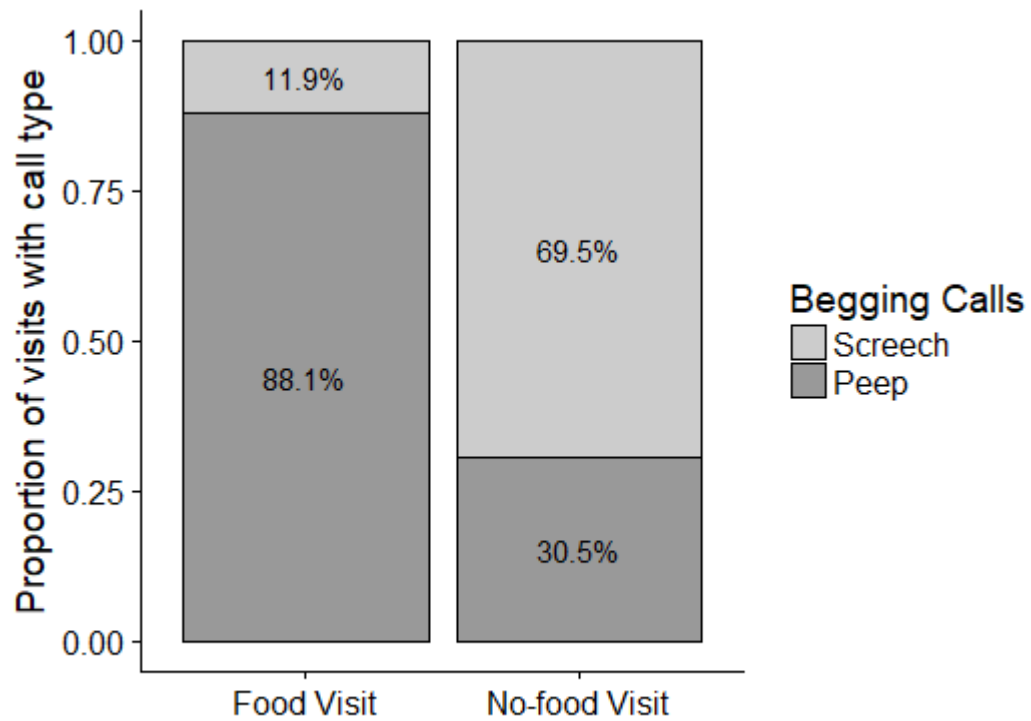


Figure 5.2 Atlantic puffin chicks emit peep calls more frequently in food visits and emit screech calls more frequently in no-food visits, during an experimental study conducted in 2011 and 2012 on Gull Island, in the Witless Bay Ecological Reserve, Newfoundland and Labrador.

Table 5.1 Mean proportion of screech calls (\pm SE) for food and no-food visits for the before (BFS) and after (AFS) food supplementation period for experimental Atlantic puffin chicks (N=16) and the early and late period for control chicks (N=3), during an experimental study conducted in 2011 and 2012 on Gull Island, in the Witless Bay Ecological Reserve, Newfoundland and Labrador.

	BFS/Early	AFS/Late
Food visits		
Experimental chicks	$0.17 \pm 0.03^*$	$0.12 \pm 0.05^*$
Control chicks	0.07 ± 0.05	0.06 ± 0.04
No-food visits		
Experimental chicks	0.71 ± 0.07	0.65 ± 0.09
Control chicks	0.49 ± 0.27	0.42 ± 0.30

* Significant difference, $p < 0.05$

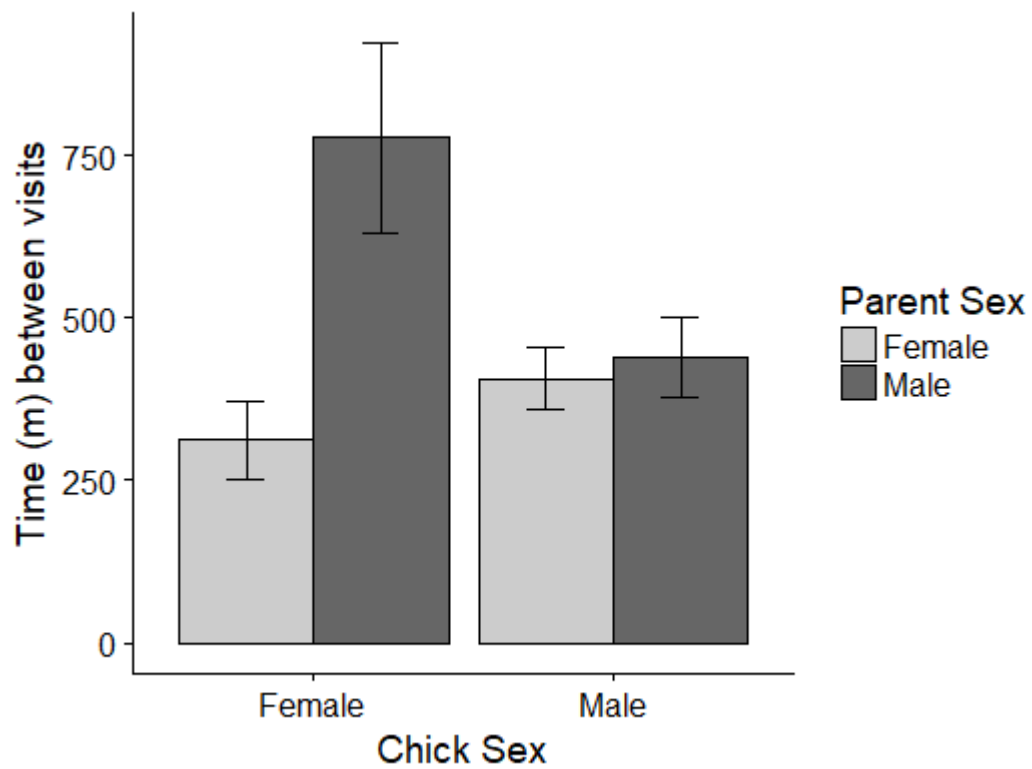


Figure 5.3 Atlantic puffin male parents take longer (in min \pm SE) to return with food between visits than female parents when feeding female chicks, during an experimental study conducted in 2011 and 2012 on Gull Island, in the Witless Bay Ecological Reserve, Newfoundland and Labrador.

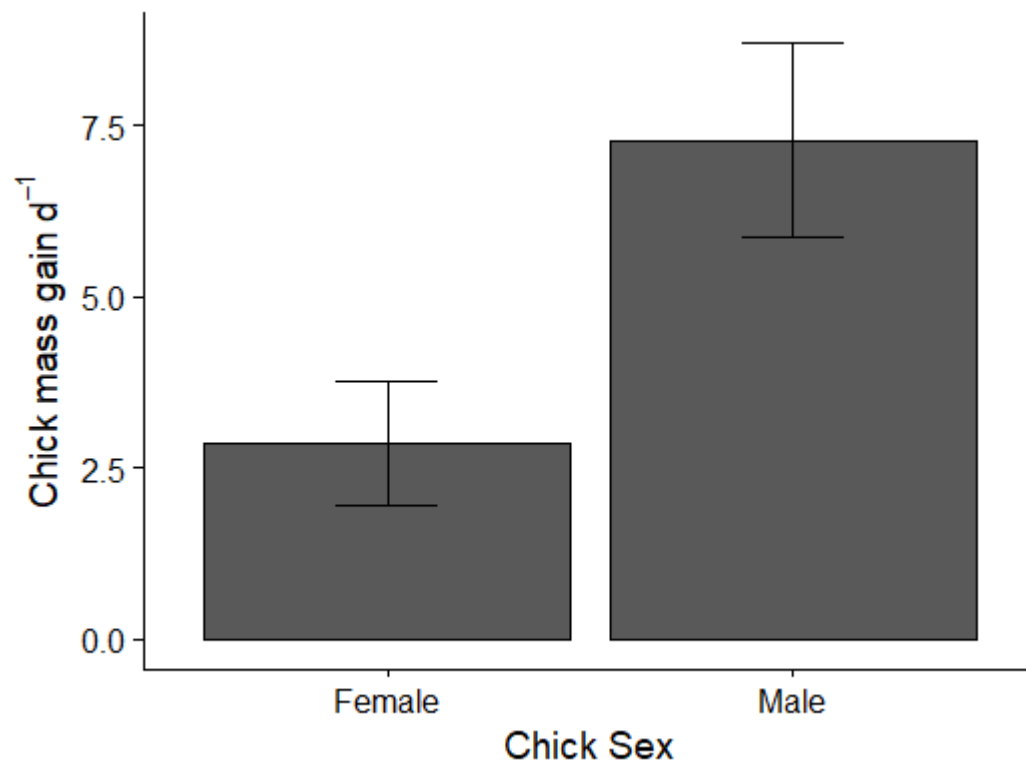


Figure 5.4 Atlantic puffin male chicks gained more daily mass (g/d, \pm SE) than female chicks during the food supplemented period, during an experimental study conducted in 2011 and 2012 on Gull Island, in the Witless Bay Ecological Reserve, Newfoundland and Labrador.

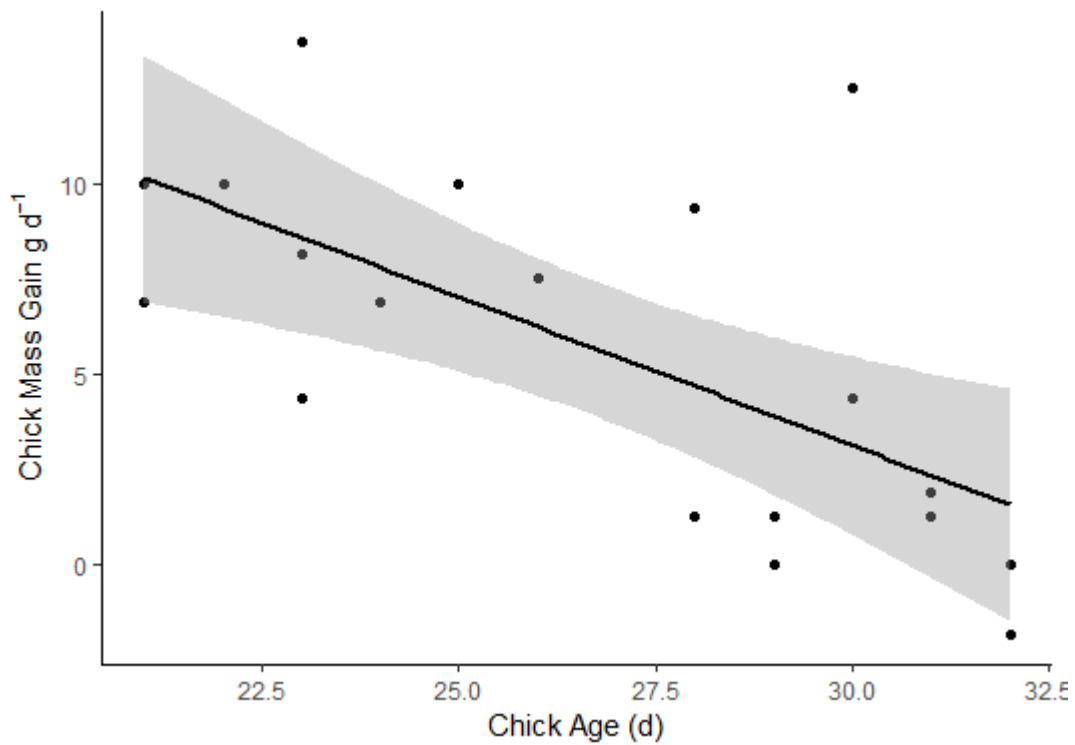


Figure 5.5 Atlantic puffin chick daily mass gain (g/d, 95% confidence intervals) was inversely related to chick age (in d) near the end of the experimental study (age range between 21 and 32 days old, $n = 19$), during an experimental study conducted in 2011 and 2012 on Gull Island, in the Witless Bay Ecological Reserve, Newfoundland and Labrador.

5.5 DISCUSSION

As identified in Rector et al. (2014), puffin chicks in this study made two distinct begging calls: screeches and peeps. These results support the findings of Rector et al. (2014) that chicks are more likely to emit screech calls in a higher proportion of no-food visits than during visits in which parents provide food. After food supplementation, the

proportion of screech calls at food visits decreased. Contrary to our predictions, food supplementation did not reduce the proportion of screech calls at no-food visits, and there was no difference in the proportion of no-food visits with screech calls between the good and poor foraging year. Parents did return to feed their chicks sooner between visits in the good foraging year of 2012 compared to the poor foraging year of 2011 and were quicker to return to the burrow with food during the pre-supplemented period compared to the food supplemented period. Whether a chick screeched or not during a visit did not appear to affect how quickly a parent returned to the burrow with food. Male parents with female chicks took longer to return with food than female parents, however there was no difference in the time it took either parent to return with food if their chick was male. Even though male chicks gained more mass than female chicks over the food supplementation period, both male and females chicks consumed the same amount of food.

The proportion of food visits with screech calls decreased after food supplementation, whereas the proportion of screech calls during no-food visits remained unchanged. This reduction demonstrates that the increased food intake by chicks may have decreased their hunger levels enough for them to not emit screech calls when food was provided, but to still signal hunger when parents visited with no food. A reduction of screech calls during food visits after food supplementation is similar to findings by Rector et al. (2014), but there was still no reduction of screech calls in no-food visits, even though there were changes made to the experimental protocol by increasing the supplemented food from one capelin to two capelin in the current study, as well as lengthening the supplemental period from six to eight days. Therefore, it was expected

that the increase in supplemental food would decrease chick hunger levels between food visits and chicks would be less likely to screech during no-food visits. It was also expected there would be a lower proportion of screech calls during no-food visits in the good foraging year compared to the poor foraging year, as chicks were provisioned more. However, the proportion of visits with screech calls did not differ between years. Although fed better in 2012 compared to 2011, chicks were apparently still not fed to satiation and therefore they still signaled to parents that they were hungry. Food supplemented chicks gained more mass than control chicks in another study in this colony during the same years (see Chapter 2) which is contrary to most other food supplemented studies on puffins (Hudson 1979, Wehle 1983, Cook & Hamer 1997, Wernham & Bryant 1998, Gjerdrum 2004, Dahl et al. 2005) suggesting that even with food supplementation, parents could not completely satisfy their chick's nutritional needs.

The time from one visit to the next feed by the same parent was shorter in 2012 compared to 2011, suggesting that prey were likely closer to the colony or more abundant in 2012. Time between visits was also shorter during the pre-supplementation period compared to the food supplementation period. The proportion of chick screech calls at food visits was reduced after food supplementation, likely indicating to parents that chicks were being fed more often by the other parent, allowing parents to spend more time away from the burrow to forage. The occurrence of begging calls did not appear to influence the time it took for parents to return to the burrow with food. Even if screech calls from chicks are an indication of hunger or need, parents may not be able or willing to respond to this signal by bringing food to the burrow right away. Food resources may not be readily available, or parents may be in poor condition and may spend more time

foraging for themselves, therefore providing the minimal nutritional requirements to chicks. Since it is not possible to immediately provision chicks upon solicitation, as is the case with regurgitating species, begging calls may be used by parents as a more cumulative indicator of chick nutritional status. Begging over multiple visits may be a better indication of chick condition and may elicit a response from parents over time.

In this study, the sex of offspring was related to how quickly their male parents returned to the burrow with food. Male parents took longer to return with food than female parents when their chick was female, while parents of male chicks did not differ in their return time. Although the sample sizes are small, the response from male parents compared to their female partners was distinctly different, suggesting that females may be investing more in provisioning effort than males, as seen in Chapter 3. Longer trips away from the burrow could be related to male parents investing more in self-maintenance, which corresponds with female parents having higher physiological costs and higher provisioning rates than males (see Chapter 3 and 4).

Male chicks gained more mass over the study period than female chicks despite male and female chicks receiving the same amount of food over the study period. There could be several explanations for this. Firstly, there could be developmental differences between male and female chicks during early development. Sex-specific growth in structure and mass was identified in black-tailed godwit *Limosa limosa limosa* chicks during the pre-fledging period (Loonstra et al. 2018). Godwits are sexually dimorphic though, and adult puffins are nearly monomorphic in size, with males being just slightly larger on average (Bond et al. 2016). However, this small difference in size could select for faster growth in pre-fledged males. Secondly, although male chicks gained more mass

than female chicks in this study, the sample size was small, and the measured mass gain was over an eight-day period. In a similar supplemental feeding study (see Chapter 2), male and female chicks did not differ in their mass gain. This other study was in the same colony in the same years but was conducted over a longer period of time of 14 days and the sample size was larger with approximately 50 chicks in each year. The result of no sex difference in chick growth suggests that the sex difference in mass gain in this current study may not be representative of the population and there may be other variables influencing this outcome, such as the measurements being taken over different periods of development.

Differences in mass gain between male and female chicks could also be due to differences in the structure of vocalizations, as shown in studies of Cory's shearwaters *Calonctris diomedea* (Bretagnolle & Thibault 1995, Quillfeldt et al. 2007). However, an examination of bout-level and structural characteristics of chick vocalizations in this study, such as screech bout duration and maximum frequency of calls, showed that there were no significant differences in these measures between male and female chicks (Taylor 2017). These results indicate that the intensity and quality of begging do not differ between males and females and therefore no sex-specific qualities in the begging vocalizations would exist that would affect the amount or frequency of food provisioned by parents. There should also be no difference between sexes in the energy expenditure of begging during parental visits. Begging was only quantified when parents were present or just outside the burrow; however, chicks also beg during times when a parent is not present (personal observation). Therefore, some chicks may have expended more energy begging than other individuals when their parents were absent. Similar to the captive

canary study (Kilner 2001), female chicks may have spent more time begging, even though they were provided with the same amount of food, and therefore they incurred growth costs. This extra energy expenditure may have influenced the difference in mass gain between males and females and if female chicks were begging more when parents were not present, this may have contributed to the lower mass gain. This study demonstrates that although screech begging calls do provide information to parents on their chick's hunger levels, begging calls may be used more as a cumulative indicator of chick nutritional status and begging may be costlier to chicks when parents are unable to respond adequately.

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CHAPTER 6 – GENERAL DISCUSSION

Seabirds are known to be one of the best indicators of the health of our oceans, providing evidence of ecosystem effects of global climate change that may not yet be visible to humans (Cairns 1988). They are highly adaptable to environmental changes, but there are costs to responding to these changes that can have long-lasting effects on their survival and reproductive success. The goal of this thesis was to better understand how changing environmental conditions can affect the behaviour and physiology of breeding Atlantic puffins, one of the more prominent alcid seabird species whose global populations are declining. This thesis includes two supplemental feeding experiments conducted during years when foraging conditions differed. This variation in food availability enabled me to evaluate how parents and chicks respond both behaviourally and physiologically to different levels of food availability.

6.1 SIGNIFICANT FINDINGS

Parents provisioned their chicks during only 56% of burrow visits, while in the other 44% of burrow visits parents brooded chicks, performed burrow maintenance, socialized, and presumably obtained information about the condition of their partners and chicks. Parents provisioned chicks more food in the year when prey seemed more available, indicating that parents need to balance provisioning with self-maintenance when food is scarce. Sex differences in parental investment emerged when prey was less available, or chicks were not food supplemented. Females invested more in provisioning

and had higher physiological costs than males when food conditions were poor. Beta-hydroxybutyrate (BUTY) levels of female parents were higher when chicks were not food supplemented, suggesting that BUTY levels can measure short-term changes in condition. Corticosterone (CORT) levels remained unchanged, regardless of food conditions, suggesting that CORT levels may not mediate foraging challenges for puffins as it does other seabirds. Chicks may have provided parents with information about body condition by begging, but parents appeared to be unable to respond by increasing their provisioning effort, perhaps due to the generally poor feeding conditions in the years of this study. Chick growth is therefore dependent on prey availability and under extremely poor environmental conditions chicks can be abandoned by their parents (as in 2011). Although there were differences in chick mass gain between sexes, provisioning effort by parents did not differ, suggesting that differences in mass may be related to the developmental period.

6.2 LIMITATIONS TO RESEARCH

Unfortunately, a thesis like this cannot be done in a vacuum or a laboratory setting where all conditions are controlled. There were some aspects of my research that I would improve upon if similar studies were to be done in the future. Firstly, the behavioural and physiological measures were conducted on two separate study plots with separate individuals. Integrating both measures in the same study would allow me to draw more concrete conclusions with greater control over individual differences. However, this integration would have been difficult to do in these studies because of the limited sample

size (small number of burrow cameras) in the behavioural study and there were also initial concerns about the effects of investigator disturbance (Rodway et al. 1996).

Secondly, prey type and quantity were measured as accurately as possible in this study, but the nutritional value of the prey may differ more than I presumed. Studies investigating long-term changes in prey size (Wanless et al. 2004) and the nutritional value of prey (Wanless et al. 2005) suggest that the nutritional value of certain fish can change over time. Therefore, measuring the nutritional value in combination with the prey type and quantity would be a better indication of the energetic value of prey items.

Finally, I had initially intended to study the same burrows and parents for consecutive years, to better understand the repeatability of behaviour and carryover effects. However, this proved to be more difficult than I thought, as parents often dug burrows deeper every year and were not easily reachable. As well, some burrow markers were lost over winter and therefore identifying the same burrows was not always easy. Repeatability of provisioning effort differed between sexes of individual house sparrows *Passer domesticus* (Nakagawa et al. 2007). However, contribution effort towards provisioning in little penguins *Eudyptula minor* did not differ between sexes, and instead individuals were consistent across years (Saraux et al. 2011). Recapturing and studying the same individuals in multiple years would allow for a better understanding of the role of individual differences and mate strategies within puffin pairs, although likely at a cost to sample size.

6.3 FUTURE DIRECTIONS

The Witless Bay Ecological Reserve is home to the largest breeding colony of Atlantic puffins in North America. It is an ideal place to study puffins because of its size and location in relation to the mainland, making logistics for field studies relatively easy. It is also an ideal place to study puffins because it is one of the few breeding colonies in the world where populations are steady or increasing (Wilhelm et al. 2015). Global populations have seen a steady decline in recent years, to the extent they are listed as a Vulnerable on the International Union for Conservation of Nature (IUCN) Red List (Birdlife International 2017). Taking advantage of a healthy population to study various contributing factors that relate to survival and productivity can help conserve the population and better manage the ecological reserve, if this population follows the global trend. Rising temperatures in the Northwest Atlantic Ocean will inevitably occur (Saba et al. 2015) and the ecosystem structure will continue to change (Buren et al. 2014), further reducing prey abundance and availability near the colonies. Advances in technology have contributed to the understanding of foraging behaviour of seabirds, and GPS tracking devices can be used to investigate the distances that puffin parents need to travel to find prey during chick rearing. This information would provide a better idea of the energetic expenditure associated with foraging. In addition, measuring other physiological biomarkers, such as triglycerides (TRIG) could contribute to the understanding of the costs of daily energy expenditure. Increased levels of TRIG indicate fat deposition and good body condition, which provides contrasting information to that of BUTY levels (Guglielmo et al. 2005, Cerasale & Guglielmo 2006), and would be an additional

biomarker for condition, especially when foraging conditions are good. However, with historically deteriorating foraging conditions, measuring TRIG levels may only confirm the information provided by measuring BUTY. Finally, to have a more complete understanding of the consequences of low prey availability for chick-rearing parents, all reproductive phases need to be considered. As seen in Rector et al. (2012), CORT levels were not different between sexes in any individual breeding stage; however, females had higher overall CORT levels across all breeding stages.

Not enough is known about puffins during the winter migration and whether there are sex differences in migration and winter foraging strategies. A study on winter migration of breeding pairs found that the foraging effort of females, but not males, best predicted breeding success in the following season (Fayet et al. 2017). Females that spent more time foraging during the winter were likely in better condition when they returned to breed, and therefore, were able to invest more in offspring care. Females that fed at higher trophic levels over winter also produced larger eggs (Kouwenberg et al. 2013). Females may already invest more in reproductive effort prior to incubation with egg production, and therefore, they may place a higher value on current offspring than male parents. There is no evidence to suggest extra-pair copulations are common and so paternity uncertainty should not result in males placing lower value on offspring than females (Creelman & Storey 1991, Anker-Nilssen et al. 2008). There may not be a conclusive reason to explain why female parents invest more in provisioning effort than male parents. However, this thesis does illustrate that examining the behaviour and physiology in this already well-studied seabird may elicit more questions than answers. For a burrow-nesting seabird that lives hidden during the breeding season and escapes on

the expansive ocean over winter, continued research is required to uncover fully the secret lives of puffins.

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